THE TAPHONOMY OF INSECTS

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ABSTRACT

Decay experiments were conducted on a range of insect morphotypes (Coleoptera: *Coccinella* septum-*punctata*, *Tenebrio molitor*; Diptera: *Calliphora vomitoria*; Blattodea: *Periplaneta americana*; Orthoptera: *Acheta domestica*; Lepidoptera: *Ephestia kuehniella*; Hymenoptera: *Formica cunicularia*) under laboratory and natural conditions. The morphological sequence of decay and the fate of the biomolecules of the cuticle were recorded. All insects disarticulate in a comparable fashion: breakdown of internal tissue and swelling of the abdomen; slumping of internal tissue and its leakage from the body orifices; rupture and disintegration of the abdomen and complete loss of internal matter; growth of microbial films and their control of further disarticulation; disarticulation of appendages (limbs, at the coxae→ antennae→cerci and oviposter→wings, which begin to disintegrate prior to detachment); finally, disarticulation of the thorax and head.

Internal tissue begins to breaks down quickly (2 weeks). However, the cuticle can persist for up to 62 weeks under laboratory conditions. Under natural conditions the proteins of the cuticle begin to breakdown after 10 weeks, producing characteristic vacancies in the endocuticle. The vacancies increase in size with time, and gradually reveal the chitinaceous microfibrils.

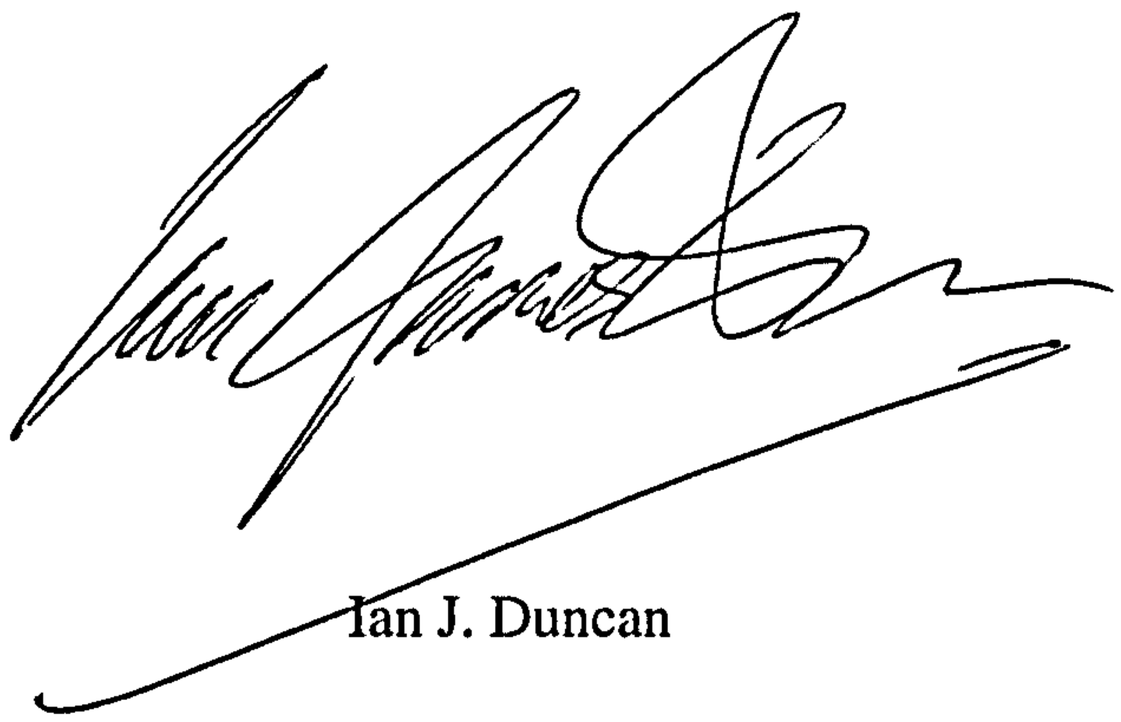
Experiments to replicate mechanical disarticulation were conducted on live and decayed cockroaches in a rotating flume. Live cockroaches are adept at avoiding drowning and survive for up to eight hours. Carcasses disarticulate in a series of stages similar to those noted in still water. Disarticulation of the recently dead cockroaches is a protracted event. Decayed specimens disarticulate more readily, but there is little to distinguish the disarticulation sequence of specimens introduced after varying stages of decay. The results were used to show that the disarticulation state of the cockroaches of Writhlington (U. Carb.), S.W. England could not be explained by decay or turbulence acting alone or in tandem. Predation is suggested as a possible explanation.

The results of these experiments were applied in seven taphonomic case studies: Mazon Creek, Illinois (U. Carb.); Weald, S.W. England (Cret.); Green River, Colorado (Eo.); Bembridge, Isle of Wight (Eo.); Riversleigh, Australia (Mio.); and Rancho La Brea (Quat.). These biotas include the most common modes of preservation: siderite concretions, calcification, phosphatization, and altered and original organics.

Early phosphatization at Riversleigh has preserved original cuticle structure at a resolution of microns. The insects of the Mazon Creek and the Weald reveal apatite in association with calcite. The cuticle structure of the Wealden insects is replicated by apatite, but calcite preserves only gross structure. Although recognizable structure is absent in the Mazon Creek insects, the presence of these authigenic minerals within the carcass suggests that fossilization may not be entirely due to concretionary growth (*e.g.* see Baird *et al.* 1986).

Insects are commonly organically preserved. The cuticle of the Green River and Bembridge insects is highly altered to a series of aliphatic compounds. The Bembridge specimens preserve detailed structure of the cuticle but those of the Green River preserve only limited original structure. The insects of Rancho La Brea are unaltered and retain original chitin, although the protein component is highly degraded.

I declare that the work contained in this thesis is my own,
except where otherwise stated.



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INSECTA

1.1 INTRODUCTION

Hexapods (of which 99.5% are insects) are the most diverse of arthropods, and dominate the planet, both in terms of diversity and abundance. Over 876,200 insect species have so far been described (Labandeira and Beall 1990). However, ultimate species richness is unknown, with estimates ranging from less than five million to in excess of 80 million - around half of global species diversity (Wheeler 1990; Gullan and Cranston 1994).

1.2 CLASSIFICATION

The superclass Hexapoda consists of all six-legged arthropods. The origin and phylogenetic history of the group is far from resolved. A number of possible ancestors have been advanced, *e.g.* annelid (Walton 1927); trilobite (Handlirsch 1908); decapod crustacean (Müller 1864; Hansen 1893; Carpenter 1903, 1905; Crampton 1920, 1928; Tillyard 1930; C.S.I.R.O. 1991, Gullan and Cranston 1994); Collembola through Protura (Tillyard 1930); and Symphyla (Packard 1873; Imms 1936; Snodgrass 1938, 1952; Sharov 1966). Unfortunately, the fossil record is inadequate to resolve this question (Carpenter 1992), and a solution is perhaps most likely to emerge from current molecular studies (Gullan and Cranston 1994).

The diagnostic features of the Hexapoda reflect their unique tagmosis (specialization of successive body segments) (Fig. 1.01). The head is composed of six segments (reflected in the mouthparts), with a pre-oral pair of antennae and dorsolateral compound eyes. The thorax is composed of three sclerotized segments, each with a six-segmented leg. (The legs of primitive insects comprised up to eleven-segments). The abdomen is composed of eleven segments.

The Hexapoda is divided into four extant classes; **Protura, Collembola, Diplura** and **Insecta**, and a single extinct class, **Monura**. Until recently the first three were united as the 'Entognatha', an assemblage based largely on the similar morphology of the mouthparts, which are enclosed in folds in the head. However, this condition is now believed to have evolved convergently in these groups (Manton 1969a). The Insecta has exposed mouthparts (ectognathy).

The Insecta are divided into the informal grouping **'Apterygota'** and the infraclass **Pterygota** (Fig. 1.02). The Apterygota are the primitively wingless insects, Archaeognatha (bristletails) and Thysanura (silverfish). Formerly united as a single

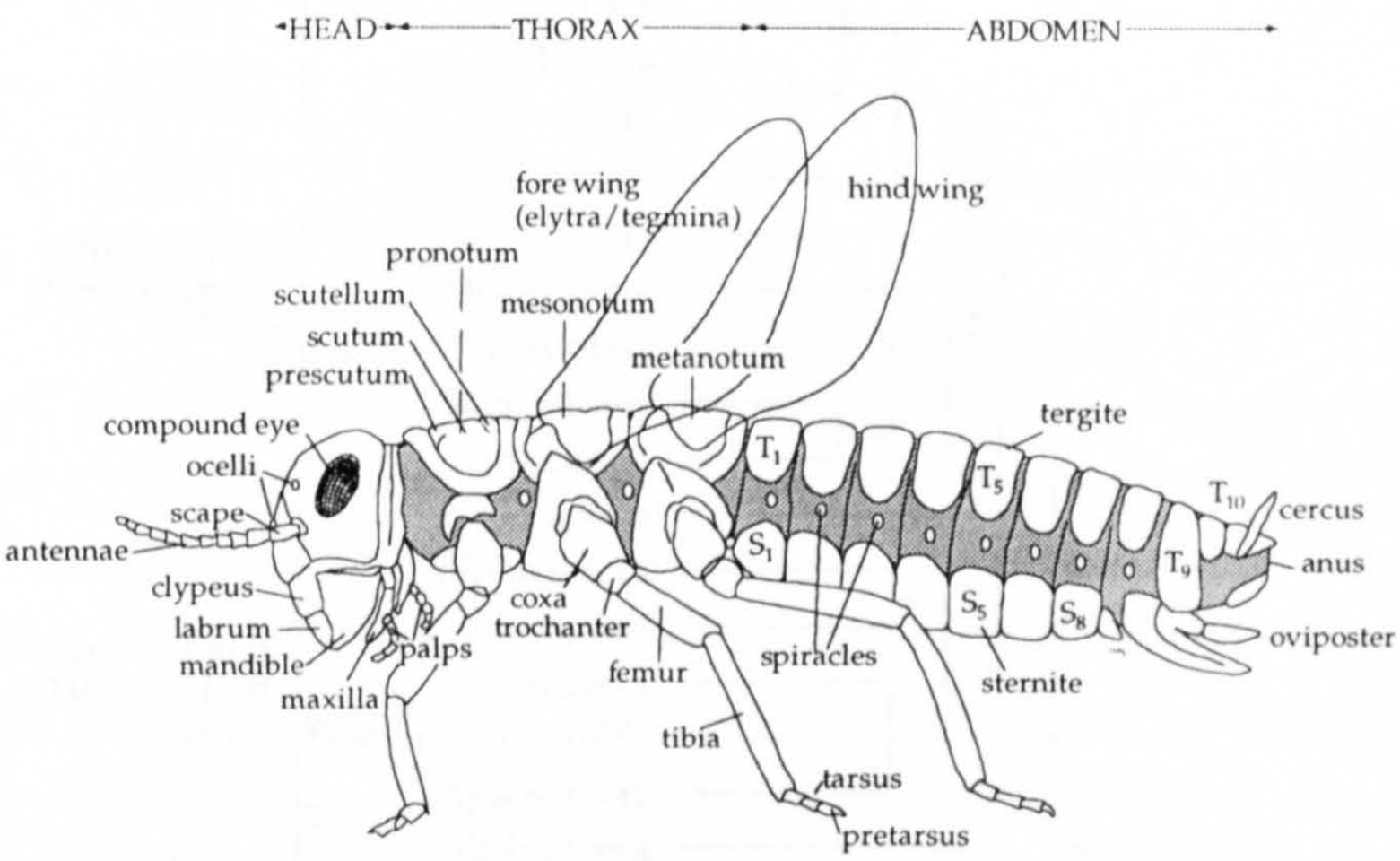


Figure 1.01 Lateral view of typical female insect. (After Carpenter 1992).

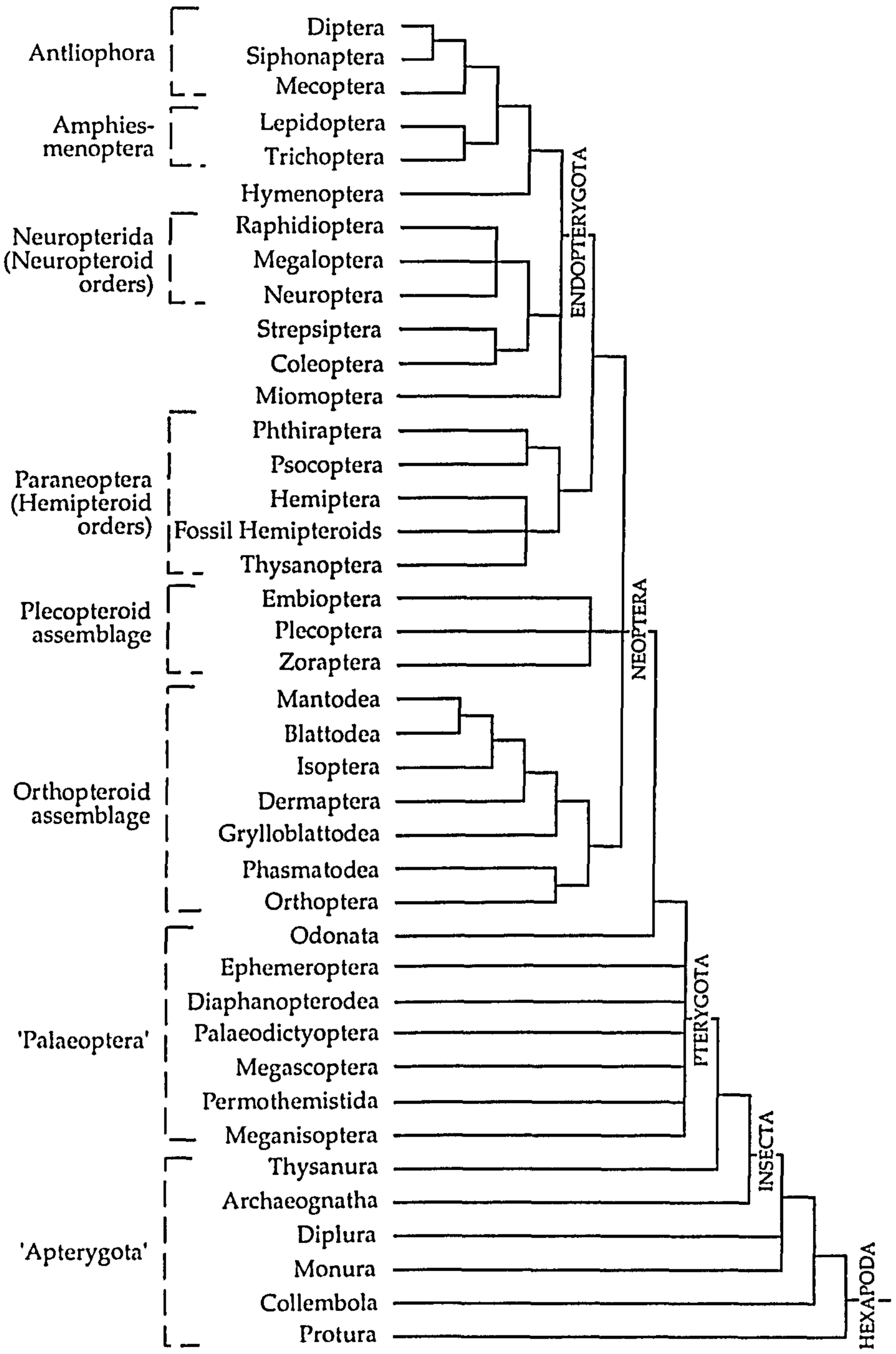


Figure 1.02 Cladogram of postulated relationships of extant and extinct insect orders. (After Gullan & Cranston 1994; Kukalová-Peck 1991).

taxon (based on shared primitive features), recent interpretation of the morphological data place the Thysanura as the sister group of the Pterygota, with the Archaeognatha and fossil Monura as more basal groups (Gullan and Cranston 1994). The Pterygota are the primarily winged or secondarily apterous taxa, and as such include the great majority of the Insecta (~99%) (Gullan and Cranston 1994).

The Pterygota was formerly divided into the **Palaeoptera** (or primitive insects, which are unable to fold their wings against their body when at rest) and the **Neoptera** (which could). However, on the basis of molecular evidence the Pterygota is now divided into three Divisions (Fig. 1.02); **Ephemeroptera** (also an order); **Odonata** (also an order); and the **Neoptera.** The Palaeoptera is recognized only as an informal grouping of extinct orders (Palaeodictyopterodea, Protodonata, Megascoptera, Protorthoptera, Diaphanoptera and Permothemistida: Kukalová-Peck 1991).

The phylogeny (and hence classification) of the neopteran orders is still the subject of debate, mainly concerning (a) the placement of many extinct orders erected on the basis of limited (and often fragmentary) material, (b) the position of the Plecoptera, (c) the composition of the orthopteroid and blattoid groups or orders, and (d) the relationship of the highly derived Siphonaptera and Strepsiptera (Gullan and Cranston 1994).

The Neuroptera may be further subdivided into the **Endopterygota,** a monophyletic group in which the wings form within pockets of the integument, with eversion taking place only at the larval/pupal moult. This group includes the informal ranks **Antiliophora** (Diptera, Siphonaptera, Mecoptera), **Amphiesmenoptera** (Lepidoptera and Trichoptera), **Neuropterida** (Raphidioptera, Megaloptera and Neuroptera) as well as the orders Strepsiptera, Hymenoptera and Coleoptera. The other neuropteran orders are also informally grouped into the **Paraneoptera** or **hemipteroid** orders (Phthiraptera, Psocoptera, Hemiptera and Thysanoptera), the **plecopteroid** assemblage (Embioptera, Plecoptera and Zoraptera), and **orthopteroid** assemblage (Mantodea, Blattodea, Isoptera, Dermaptera, Grylloblattodea, Phasmatodea and Orthoptera).

1.3 MORPHOLOGY OF THE INSECTA

1.3.1 Introduction

Detailed accounts of insect morphology are available in such basic works as *The Insects of Australia*, by the C.S.I.R.O. (1992) and *Imms' General Textbook of Entomology*, 10th ed., edited by Richards and Davies (1977). The following discussion is a generalization from such sources and should be read in conjunction with Fig. 1.01.

1.3.2 Head

The rigid head capsule bears the mouthparts, compound eyes, a pair of sensory antennae and, in many insects, three **ocelli** (light-sensitive, simple eyes).

Typically, the mouthparts are directed ventrally (**hypognathous**), although sometimes anteriorly (**prognathous**) as in many Coleoptera, or posteriorly (**opisthognathous**) as in Homoptera. The six-part segmentation of the head is most clearly demonstrated by the mouthparts (Snodgrass 1935). In omnivorous insects, such as Blattodea, Orthoptera and Dermaptera, the mouthparts are of a biting and chewing type (**mandibulate**) and resemble the probable basic design of ancestral pterygote insects (Carpenter 1992). Extreme modifications of basic mouthpart structure reflecting feeding specialization occur in most Lepidoptera, Diptera, Hymenoptera and a number of the smaller orders.

The compound eyes are generally large and prominent, affording a broad visual field. Each eye is divided into many individual units called **ommatidia** which consists of a circular lens overlying a conical crystalline lens above eight elongate nerve cells (see Chapter 7, Plate 7.5e). The inner part of each cell contains the visual pigment(s) of the central **rhabdom**. The nerve cells are clustered around the longitudinal axis of each ommatidium and are surrounded by a ring of light-absorbing pigmented cells, which isolates each ommatidium.

The three ocelli, the median and two laterals, typically lie in a triangle on top of the head. Each is a single visual unit, which may enhance light detection or register cyclical changes in light intensity.

The antennae are mobile, segmented, paired appendages. Primitively they are eight-segmented, but they may be reduced, almost absent, or variously modified, and as such are important in taxonomy. They may possess numerous chemo-, mechano-, thermo-, or hygro-receptors.

1.3.3 Thorax

The thorax is composed of three segments termed the **prothorax, mesothorax,** and **metathorax**. Although they are similar in size and complexity in primitive insects (Carpenter 1992), in most winged insects the meso- and metathorax are enlarged relative to the prothorax, forming a **pterothorax**, which bears the wings and associated musculature. Wings occur only on the second and third segments in extant insects, although some extinct Palaeodictyoptera, Protorthoptera and Ephemeroptera have prothoracic winglets (Carpenter 1992). Almost all nymphal and adult insects have three pairs of thoracic legs, one pair per segment. Typically the legs are used for walking, although various other functions and associated modifications occur.

The tergal plates of the thorax are termed **nota**. The **pronotum** may be simple in structure, and small in comparison to the other nota, but in beetles, mantids, many bugs and some orthopterans it is expanded, while in cockroaches it shields part of the

head and mesothorax. The pterothoracic nota each have two main divisions, the anterior wing-bearing **alinotum** and the posterior **postnotum.** Each alinotum may be traversed by internal strengthening ridges which commonly divide the plate into three areas: the anterior **prescutum**, the **scutum,** and the smaller posterior **scutellum.**

Typically, each leg is comprised of six segments: the proximal **coxa, trochanter, femur, tibia, tarsus,** and **pretarsus** with claws. Abdominal legs (**prolegs**) are confined to the immature stages of holometabolous insects.

The wings are normally only fully developed in the adult, but they also occur in the penultimate stage of Ephemeroptera (Gullan and Cranston 1994). The generally membranous and transparent wings are flap-like cuticular projections supported by tubular, sclerotized veins (Holdsworth 1940, 1941, 1942). The fore wings are dorsolateral on the mesothorax, the hind wings on the metathorax. The wing veins are longitudinal, running from the wing base towards the tip, and are concentrated toward the anterior margin (see Chapter 3, Fig. 3.03). Additional supporting cross-veins join the longitudinal veins, increasing the complexity of the venation (for a detailed discussion of venation, see Wootton 1979). Venation is consistent within groups (particularly families and orders) but differs between them, facilitating classification and identification. Venation is particularly important in the classification of fossil material, since wings are more commonly and completely preserved than less sclerotized body parts (Carpenter 1992).

The basic wing condition may be highly differentiated, often involving variation in relative size, shape and degree of sclerotization of fore and/or hind wings. Examples of fore-wing modification include the thickened, leathery fore wings of Blattodea, Dermaptera and Orthoptera, termed **tegmina,** the hardened fore wing cases, or **elytra** of Coleoptera, and the **hemelytra** of Heteroptera with a thickened basal part and membranous apical part. In Diptera the hind wings are modified as stabilizers (**halteres**), while in the male Strepsiptera, it is the fore wings that are so modified.

1.3.4 Abdomen

Primitively, the insect abdomen is 11-segmented, although segment 1 may be reduced or incorporated into the thorax (as in many Hymenoptera), and usually the three terminal segments are variously modified and/or diminished. Generally, at least the first seven abdominal segments of adults (the pre-genital segments) are similar in structure and lack appendages. Spiracles are typically present on segments 1-8.

The ano-genital part of the abdomen, the **terminalia**, generally consists of the final four segments (*i.e.* 8 or 9 to the abdominal apex). Segments 8 or 9 bear the genitalia. Segment 10 is present as a complete segment in many lower insects but always lacks appendages. A pair of appendages, the **cerci**, articulates laterally on segment 11. Typically cerci are annulated and filamentous but have been variously modified (*e.g.* the forceps of earwigs) or reduced in different insect orders. The male external

genitalia are widely used in species identification. The female terminalia include structures which facilitate copulation, and an external egg-laying structure termed the **ovipositer.**

1.4 CUTICLE

1.4.1 Introduction

The cuticle is a key contributor to the success of the Insecta. This inert layer provides the strong exoskeleton of the body and limbs, the **apodemes** (internal supports and muscle attachments) and the wings of pterygote insects, and acts as a barrier between living tissues and the environment. Internally the cuticle lines the tracheal tubes, some gland ducts and the foregut and hindgut of the digestive track (Gullan and Cranston 1994).

Cuticle is highly variable. It may be rigid and armour-like, as in mandibles, and most of the exoskeleton of beetles, or thin and flexible as in the arthrodial membrane of larvae, and the connective tissue of adults. It may also form the most efficient rubber known, **resilin**, found in the leg joints of fleas (Neville and Roschild 1967), and the wing attachment of various insects (Weis-Fogh 1961). However, its critical function is the restriction of water loss, vital to terrestrialisation.

As a consequence of the exoskeleton's rigidity, insects must shed old, confining cuticle and form new in order to grow and develop into larger larvae, pupae or adults. A new chitinous skeleton, much folded and compressed, forms beneath the old one separated by a layer of liquid which absorbs the chitin from the old skeleton, and leaves the hard sclerotised parts connected by the thinnest of tissues. This chitin-rich liquid is then absorbed through the still permeable new skeleton back into the body. The old cuticle splits apart, usually along the dorsal midline, and the insect hauls itself out. As it does so, its liberated body begins to swell, filling out the folds in the new skin. In a short time, the chitin hardens and becomes strengthened through sclerotisation. However, the notion that insects grow intermittently with each moult is incorrect (Neville 1970). Although size increases episodically, weight increases steadily during each instar.

1.4.2 Microstructure

The outer covering of the living tissue of the insect, the **integument**, consists of two units, the **epidermis** and the **cuticle** (Hepburn 1985; Hadley 1986; Binnington and Retnakaran 1991; Binnington 1993) (Fig. 1.03). The epidermis is a single layer of cells, which lies beneath and secretes the cuticle. The cuticle itself consists of an underlying portion which consists primarily of chitin complexed with protein and a small amount of lipids, termed the **procuticle** and an outermost set of layers collectively termed the **epicuticle** which lack chitin (Evans 1984) (Fig. 1.03).

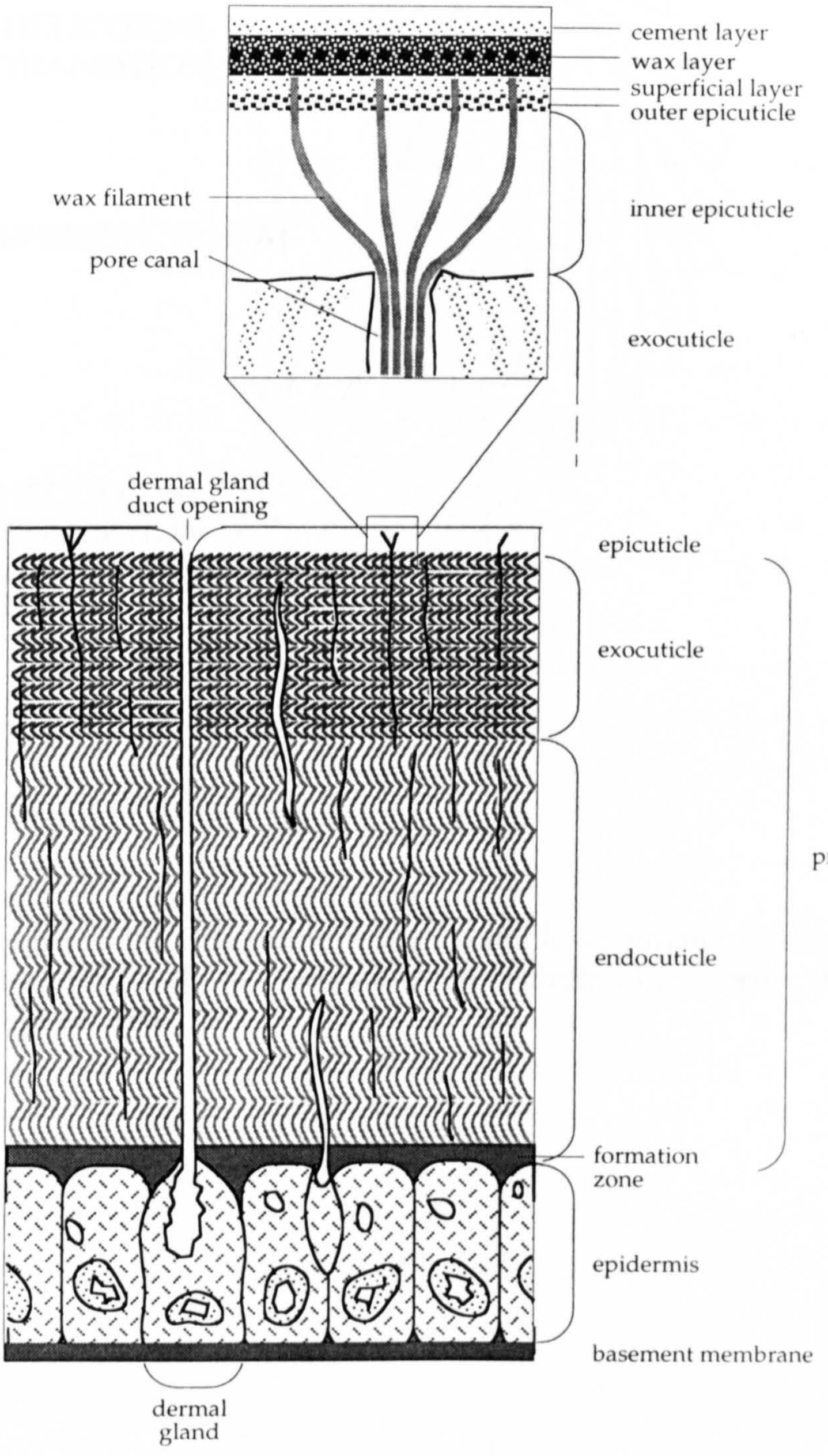


Figure 1.03 The general structure of insect cuticle; the enlargment displays details of the epicuticle. (After Gullan & Cranston 1994; Hepburn 1985; Hadley 1986; and Binnington 1993).

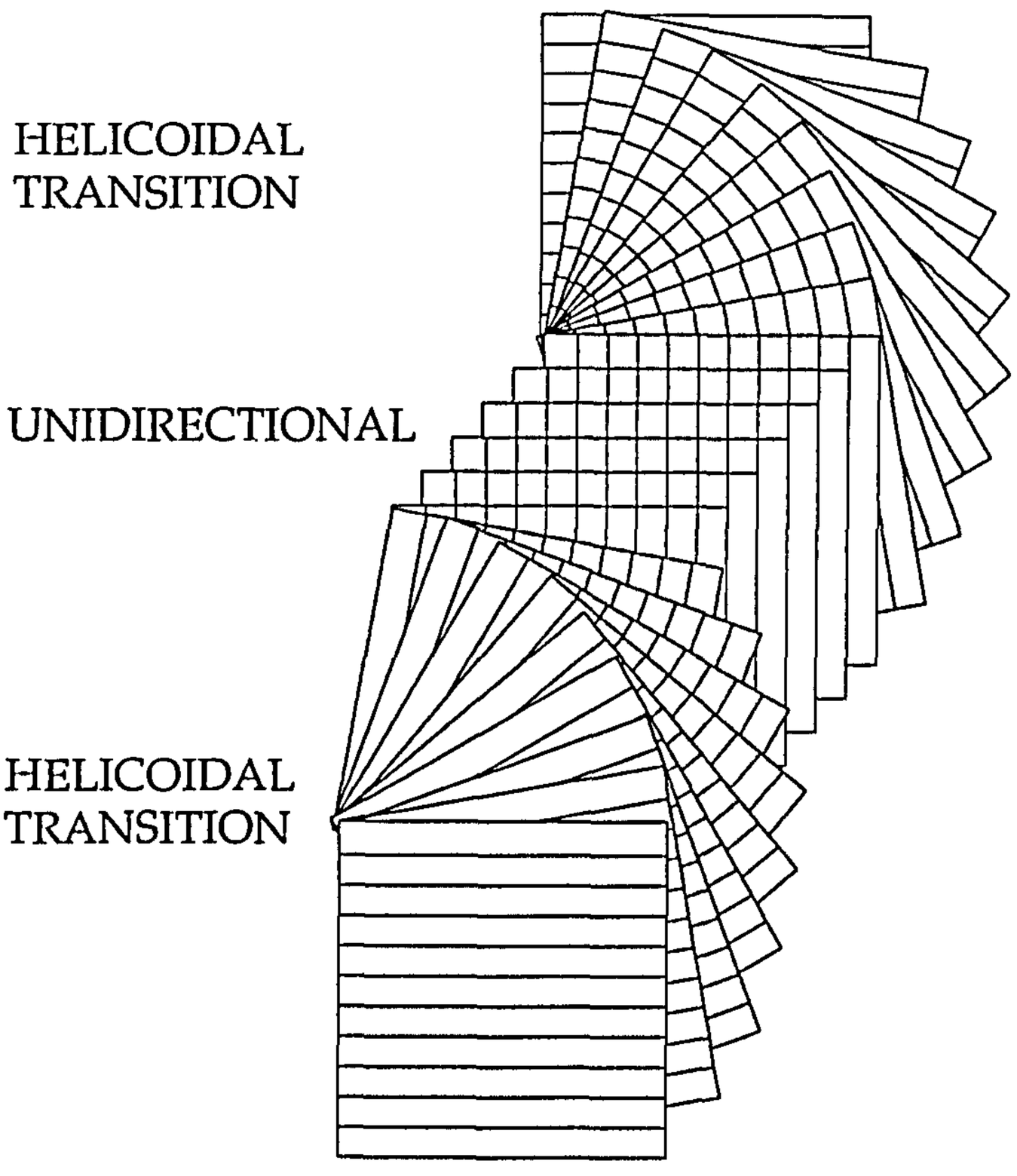


Figure 1.04. Schematic of insect cuticle displaying helicoidal and unidirectional emplacement of chitin microfibrils. After Neville 1967.

The epicuticle ranges in thickness from 3μm to 0.1μm, and may be smooth or sculpted into elaborate patterns. Three sub-layers are present: an **inner epicuticle** primarily composed of protein, an **outer epicuticle** containing cross-linked lipid and protein molecules and a **superficial layer**, probably glycoprotein (Fig. 1.03). In many insects the superficial layer is covered by a lipid or wax layer and external to this, a discrete cement layer. The chemistry of the epicuticle is vital in preventing dehydration, a function derived from water-repelling (hydrophobic) lipids, especially hydrocarbons. These compounds include free- and protein-bound lipids, with the outermost waxy coating colouring the external surface of some insects. Other cuticular patterns, such as light reflectivity, are produced by various kinds of epicuticular surface microsculpturing, such as close-packed, regular or irregular tubercles, ridges or tiny hairs. The exact lipid composition and waxiness can vary according to environmental and seasonal factors. Besides being water repellant, surface waxes may deter predation, provide patterns for mimicry or camouflage, repel excess rainwater, reflect solar and UV radiation, or give species-specific olfactory cues (Gullan and Cranston 1994).

The epicuticle is extensible, and lacks the strength of the supportive procuticle. The procuticle itself supports the internal organs and muscles and ranges in thickness from 10μm to 0.5mm. It is composed of two units, a thicker **endocuticle** overlain by a thinner **exocuticle**, differentiated by sclerotization of the latter (Richards 1978). The procuticle consists primarily of chitin complexed with protein. The endocuticle of many orders (Orthoptera, Blattodea, Dermaptera, Odonata, Hemiptera, Hymenoptera) is laid down in the form of daily growth layers. Layers deposited nocturnally comprise several lamellae, while those deposited during the day are non-lamellar. Where this alteration occurs, it allows individuals to be aged (Neville 1963a).

1.4.3 Chitin

1.4.3.1 Introduction. Chitin is a major constituent of all arthropod cuticles (Muzzarelli 1977; Schimmelmann and DeNiro 1986a, b; Gooday 1990; Miller *et al.*, 1993; Kramer *et al.* 1995), as well as of other invertebrates, fungi and yeast (Kramer and Koga 1986; Gullan and Cranston 1994). An estimated 10^{11} tons of chitin are produced annually in the biosphere (Gooday 1990), most of it in the oceans. The chitin biopolymer has been studied extensively in the last 20 years, not least because it has significant commercial application (Schlotzhauer *et al.* 1976; Muzzarelli 1985; Kramer and Koga 1986; Peter 1995).

1.4.3.2 Chemistry. Chitin is an unbranched polymer of high molecular weight, an amino acid polysaccaride composed of b(1-4) linked units of N-acetyl-D-glucosamine (Cohen 1991). Chitin chains are clumped into microfibrils, and at any one level within the cuticle these are arranged in sheets aligned parallel to one another,

much like plywood (Neville 1967a, b, 1970; Retnakaran and Hackman 1985). These microfibrils are embedded in and intimately linked to a protein matrix, giving great tensile strength. In the exocuticle, each successive sheet lies in the same plane but may be orientated at a slight angle to the previous sheet, like the edges of a fanned deck of cards (Fig. 1.04), such that a thickness of many sheets produces a helicoidal arrangement (Bouligand 1965; Neville 1970). In the endocuticle, alternate stacked or helicoidal arrangements of microfibril sheets may occur, giving rise to thicker lamellae than in the exocuticle. Much of the strength of cuticle comes from the hydrogen bonding of adjacent chitin chains.

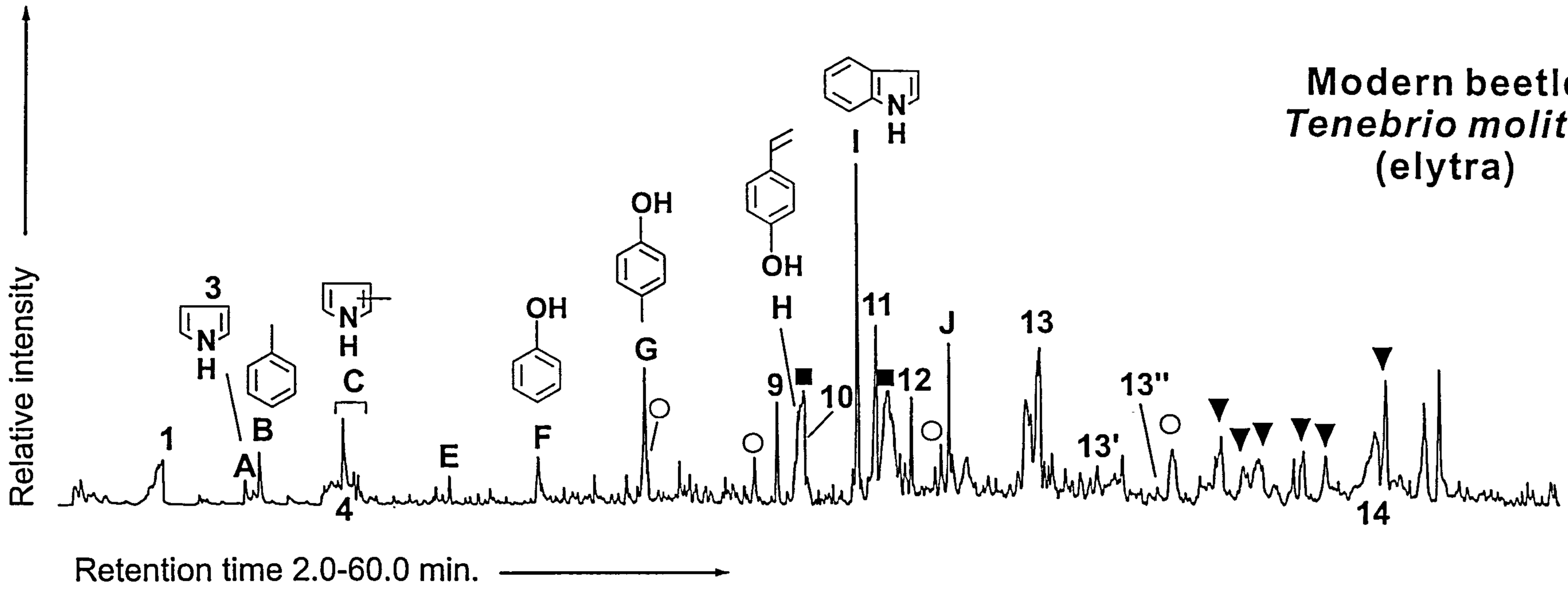
Chitin is often cross-linked with proteins via catechol and histidyl moieties (Schaeffer *et al.* 1987) in a process known as sclerotization (Kramer *et al.* 1995), an irreversible stiffening/darkening process resulting in the proteins becoming water-insoluble.

Figure 1.05 displays the minor and major components of cuticle which can be revealed using pyrolysis Gas Chromatography/Mass Spectrometry (see Appendix A1.5). The major pyrolysis products of chitin (numbers) and proteins (letters) found in modern and fossil insect cuticles are listed in Table 1.1.

1.4.3.3 Preservation. Chitin produced in the oceans undergoes extensive biodegradation within the water column, resulting in the removal of up to 90% of the mass (Gooday 1990). Biodegradation continues at the sediment-water interface and within the sediment, where anaerobic microorganisms normally decompose the remaining refractory components (Poulicek *et al.* 1985; Poulicek and Jeuniaux 1991). The decay of chitin in terrestrial environments is less well understood. Here, as in marine organisms, the preservation potential of chitin is enhanced where it is cross-linked in robust sclerotized cuticle. Recognisable quantities of the chitin monomer have been reported in Quaternary (Miller *et al.* 1993; Stankiewicz *et al.* 1997d) and Tertiary beetles. Laboratory experiments have demonstrated that, while chitin is relatively resistant to degradation, the protein components of cuticles are more readily biodegraded (Baas *et al.* 1995; see also Chapters 2 and 8). It is clear, however, that chitin only survives in a recognisable form in exceptional circumstances.

Organic remains of arthropod cuticle are abundant in the fossil record, sometimes preserving remarkable morphological detail of the surface (Butterfield 1990, 1994; Briggs and Clarkson 1989; Shear and Kukalova-Peck 1990). Early studies claimed the preservation of the chitin polymer (as evidenced by D-glucosamine) in cuticles as old as Cambrian (Carlisle 1964). However, more recent analyses have failed to find any evidence of its presence in fossils (Voss-Foucart and Jeuniaux 1972; Schimmelmann *et al.* 1988; Baas *et al.* 1995; Stankiewicz *et al.* 1997b) except for small amounts of amino sugars in the calcified skeletons of Cretaceous and Tertiary decapod crustaceans (Brumioul and Voss-Foucart 1977) and significant quantities of chitin in Quaternary

Figure 1.05 Reconstructed ion chromatograms (pyrolysis at 610°C for 10 sec) of elytra from modern mealworm beetle (*Tenebrio molitor*). Numbers indicate major pyrolysis products derived from chitin and amino acids (details in Table 8.2), m - other important components directly related to chitin polymer, n - pyrolysis products of catechol moieties, t - pyrolysis products of proteins with 2,5-diketopiperazine structure. Chemical structures are given for the most important pyrolysis products derived directly from chitin or amino acid moieties.


Modern beetle
Tenebrio molitor
(elytra)
Relative intensity
Retention time 2.0-60.0 min.
1
3
N
H
A
B
4
N
H
C
E
OH
F
OH
G
OH
H
9
10
11
12
J
13
13'
13''
14
I
N
H

12A

Peak*	MS characteristics	Compound name	Origin
(1)	60	Acetic acid	Chitin
(2)	79, 52	Pyridine	Chitin
(3, A)	67, 55	Pyrrole	Ch, Pro
(4)	59	Acetamide	Chitin
(5)	93, 66	Methylpyridine	Chitin
(6)	109, 81, 53	Methylpyridone or Hydroxypyridine†	Chitin
(7)	107, 79, 51, 78	2-Pyridinecarboxaldehyde [T]	Chitin
(8)	127, 42, 85	Acetylpyrrolidone‡ [T]	Chitin
(9)	137, 109, 95, 81, 68, 53	Acetylpyridone‡†	Chitin
(10)	125, 83, 54, 42, 53	3-Acetamidofuran††	Chitin
(11)	139, 97, 69, 42, 53	3-Acetamido-5-methylfuran††	Chitin
(12)	153, 111, 82, 42, 83	3-Acetamido-4-pyrone††	Chitin
(13,13',13")	167, 84, 55, 83, 42	oxazoline structure†	Chitin
(14)	204, 59, 101, 114, 57	1,6-anhydro-2-acetamido-2-deoxyglucose†	Chitin
(B)	92, 91	Toluene	Phe
(C)	81, 80, 52, 50	C_1-pyrrole	Hpro
(D)	104, 78, 51, 103	Styrene	Phe
(E)	95, 94, 66	C_2-pyrrole	Hpro
(F)	94, 66	Phenol	Tyr
(G)	108, 107, 77, 79	3- and 4-methylphenol	Tyr
(H)	120, 91, 65	Vinylphenol	Tyr
(I)	117, 90, 89, 63	Indole	Trp
(J)	131, 130, 77	C_1-indole	Trp

*Numbers in parentheses refer to peaks on the chromatograms (Figure 1.06)

[T] Based exclusively on interpretation of mass spectra and NIH mass library

† Follow van der Kaaden *et al.* 1984; †† Follow Franich *et al.* 1984.

Table 1.1 List of major chitin and protein pyrolysis products recognised in the pyrolysates of modern insect cuticles. Masses in bold indicate base peak and masses underlined indicate molecular weight (MW).

beetles (Miller *et al.* 1983; see Chapter 8). Even where the morphology of the cuticles in ancient fossils appears to be perfectly preserved, the original chemical integrity is highly altered, yielding an aliphatic or aromatic polymer characterised by a homologous series of alkanes and alkenes upon pyrolysis (Baas *et al.* 1995; van Bergen *et al.* 1995; Stankiewicz *et al.* 1997b). The origin of these diagenetic products and the elucidation of the chemical pathways involved are currently under investigation (Baas *et al.* 1995; Stankiewicz *et al.* 1996, 1997a, b, c). Such results prompted the conclusion that the preservation of chitin derivatives such as amino sugars and amino acids probably occur only in unusual fossilization conditions such as oil seeps (Schimmelmann *et al.* 1988; see Chapter 8). However, recent study of the Oligocene insects of Enspel, Germany has revealed significant traces of chitin in weevils (Coleoptera: Curculionidae), suggesting that the preliminary control on the preservation of these biomolecules in ancient rocks is not time but the nature of the depositional environment and the inhibition of diagenetic alteration (Stankiewicz *et al.* 1997c).

1.5 FOSSIL RECORD OF THE INSECTA

1.5.1 Introduction

The fossil record of insects is extensive (Labandeira and Sepkoski 1993; Jarzembowski and Ross 1993). Although traditionally considered inferior to the fossil record of other major taxa (see Carpenter 1992, p13), recent investigation of the family level diversity of fossil insects has demonstrated that they represent some 63-69% of extant taxa, a figure that approaches 100% for the Tertiary (Labandeira and Sepkoski 1993; Jarzembowski and Ross 1993; Labandeira 1996). This contrasts with earlier studies conducted at a species level which put the figure at around 1% (Muller and Campbell 1954). This divergence may be attributed to the shear diversity of insects at species level, and the vagaries of preservation which prevent the recognition of true 'biological species'. The shear number of insect-bearing deposits and the dearth of palaeoentomologists or neo-entomologists willing to work with fragmentary fossil material will ensure the the true species richness is not recognised for some time to come.

In most cases the fossilization of an insect is initiated when it falls into a body of water. If not consumed by scavengers or detrivores, it may be entombed in fine sediments. If diagenetic circumstances conspire it may be preserved. Although chitin and protein, the primary constituents of the insect cuticle, may persist for months after death, they are ultimately consumed by a variety of micro-organisms (Chapter 2). Commonly only the recalcitrant parts, wings and elytra, survive for any significant period of time. Therefore, the more rapid the burial, the more complete the potential fossil. However, most insects are fossilised only under very precise conditions. For this reason, the insect record is considerably biased. The absence of a family from a

fossil-bearing deposit need not necessarily indicate that the taxon did not exist during the time period represented. Temporary traps, which merely halt decay, even if for millions of years (*sensu* Allison and Briggs 1991) include amber, copal, asphalt and permafrost. While these media preserve striking specimens, they do not record a major proportion of the insect record, although the specimens may be of particular evolutionary significance. The exception is peat, a temporary trap that preserves a significant component of the Quaternary biota (Elias 1994).

1.5.2 Evolution and Occurrence

The following discussion should be read in conjunction with Table 1.2.

Few fossil insects are known from the first 60 million years of their 390-million year history (Fig. 1.06; 1.07). The earliest hexapod, the springtail (Collembola) *Rhyniella praecursor*, was recovered from the Devonian Rhynie Chert of Aberdeenshire, Scotland (Whalley and Jarzembowski 1981). Numerous fragments of other arthropods have been found in contemporaneous and younger Devonia freshwater deposits but they cannot be asigned to any living hexapod class (Carpenter 1992). The paucity of Upper Devonian and Lower Carboniferous insect remains probably results from a lack of suitable preservational environments rather than low insect diversity, since by the Upper Carboniferous fully winged insects had evolved (Wootton 1981).

PALAEOZOIC ERA

Upper Carboniferous

A massive radiation of insects must have occurred during the Lower Carboniferous (Fig. 1.06; 1.07), since by the Namurian insects were numerous and widespread (Wootton 1981). This radiation is attributed to two evolutionary advances, the advent of flight (and the origin of Pterygota), and the ability of insects to fold their wings back over the abdomen when at rest (neopterous Pterygota). Flight is probably the single most important step in the history of the insects (Carpenter and Burnham 1985). Flight provided an effective means of dispersal and escape from predators while increasing flexibility in food gathering. The origin of wings and flight remains unclear (Kukalová-Peck 1978; Rasnitsyn 1981; Kingslover and Koehl 1985, 1989; Carpenter 1992).

The ability of some insects to fold their wings, so protecting the vulnerable abdomen (wing flexing), enabled them to invade a diversity of new habitats. Unhindered by awkward outstretched wings, these insects were able to avoid predators by crawling into dense foliage or seek refuge beneath bark and stones (Carpenter and Burnham 1985; Jarzembowski and Ross 1993). In some, the fore wings were

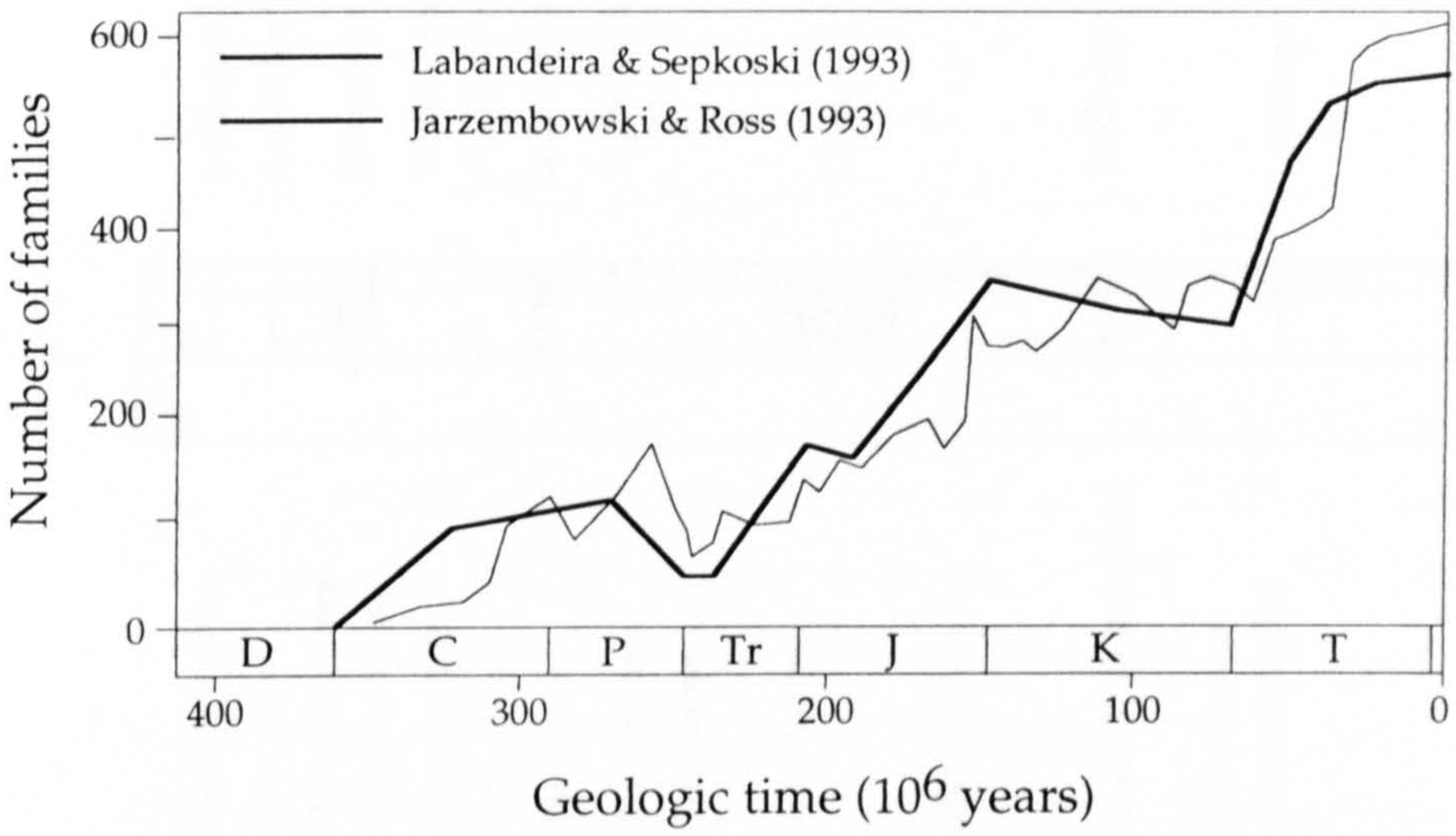


Figure 1.06 Family-level diversity of fossil insects through geological time based on the work of Labandeira & Sepkoski (1993) and Jarzembowski & Ross (1993).

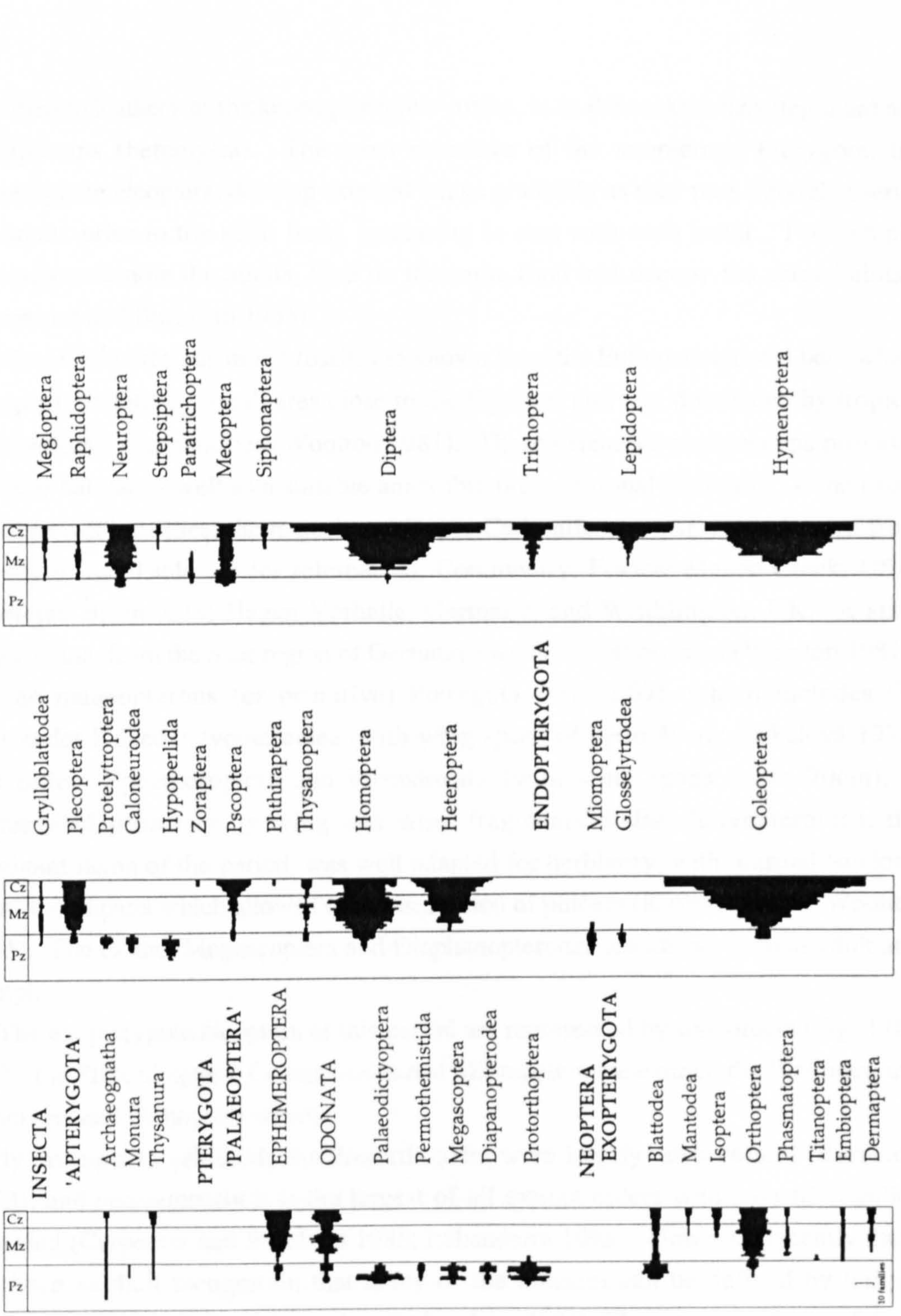


Figure 1.07 Spindle diagrams displaying diversities of fossil families within insect orders in the stratigraphical stages of the Phanerozoic. Scale bar is shown in the lower right. (After Labandeira & Sepkoski 1993).

modified to leathery or thickened protective covers, as in the cockroaches (tegmina) and hemipterans (hemelytra). The most primitive of the neopterous Pterygota, the exopterygote Neoptera, develop external wings gradually as they pass through a series of moults prior to the adult form, increasing in size with each instar. The nymphs typically resemble the adults, feed on the same food and occupy the same habitats (Carpenter and Burnham 1985).

Most Carboniferous insect fossils are known from the Euramerican coal belt, which occupied a relatively small area close to the Equator, and was dominated by tropical swamp/forest communities (Wootton 1981). These extensive coal swamps provided an ideal habitat as well as a suitable anaerobic preservational medium. Of the many fossiliferous localities, the majority of Upper Carboniferous insects are known from only five (see Table 1.2 for references): Commentry, France; Mazon Creek, USA; Kuznetzk Basin, CIS; Hagen-Vorhalle, Germany; and Writhlington, UK. A sixth major fauna, from the Saar region of Germany awaits critical revision (Wootton 1981).

The palaeopterous (or primitive) Pterygota (Fig. 1.07), which includes the superorder Palaeodictyopteroidea (with wing spans of up to 40cm: Kukalová 1970) and orders Ephemeroptera and Protodonata (with wing spans up to 70cm), is represented primarily by wing and wing fragments. Palaeodictyopteroidea, the dominant taxon of the period, was well adapted for herbivory, with unusual 'sucking beak' mouthparts which allowed the consumption of phloem (Kukalová 1970; Wootton 1981). The extinct Megascoptera and Diaphanopterodea are known both as adult and nymph.

The exopterygote Neoptera of this period are represented by five orders (Fig. 1.02, 1.07): the Protorthoptera, Caloneurodea and Miomoptera are extinct, the Blattodea and closely related Orthoptera survive.

Early attempts to subdivide the Protorthoptera were largely unsuccessful (Burnham 1983), and consequently it is the largest of all extinct orders with over 65 families recorded (Carpenter and Burnham 1985; Labandeira 1993). However, recently there has been explicit recognition that many of the families can be defined by unique characters, or allocated to other orders (Labandeira 1993). The most significant of these 'protorthopteran' taxa are ancestral hemipteroid families, which can be placed in a new order (Rasnitsyn 1980; Kukalová-Peck and Brauckmann 1993). Some of the 'protorthopterans' may even be primitive holometablous insects (Labandeira 1993). Orthopterans are similar to protorthopterans but differ in having hind legs modified for jumping (only a single family is known from the Upper Carboniferous: Carpenter 1992).

Blattodea (cockroaches) represent some 80% of all known Upper Carboniferous insects (Carpenter and Burham 1985). Preserved primarily as forewings, classification is problematic since the characteristics required for family- or generic-level determination are rarely available (Carpenter 1992; see Chapters 2 and 3). The

basic morphology of fossil cockroaches is almost indistinguishable from that of modern ones, except that the long external oviposter of the extant female is absent (Schneider 1978).

Permian

The diversity minimum of insects in the early Permian (Fig. 1.06) is considered an artifact, reflecting the scarcity of fossil-bearing freshwater outcrop (Labandeira and Sepkoski 1993).

The final major stage of insect evolution occurred around the end-Permian, with the evolution of a more complicated or indirect type of post-embryonic development among some Neoptera (Carpenter and Burnham 1985; Jarzembowski and Ross 1993; Gullan and Cranston 1994). In these insects, known as the endopterygote Neoptera (or Holometabola), wing buds develop in the immature stages, or larvae, as invaginations of the body wall. The wings are not evaginated until the insect reaches the pupal stage, a quiescent, non-feeding stage, during which considerable morphological re-organisation takes place. The larvae show little resemblance to the adults, feed on different food, and occupy different habitats.

The Permian insect fauna is better known than that of any other pre-Tertiary interval, due primarily to the work of Frank M. Carpenter and Jarmilla Kukalová(-Peck). It comprises the most morphologically diverse insect fauna known (Carpenter and Burham 1985; Wootton 1981). Our knowledge of Permian insects owes most to four faunas (Table 1.2): Elmo, Kansas, U.S.A.; the Boskovice Furrow, Moravia, Czech Republic; Tshekarda, in the Urals, C.I.S.; and the Kuznetsk Basin, southern Siberia, C.I.S.. There are also significant deposits at Belmont and Warner's Bay N.S.W., Australia (see Chapter 7).

All the insect orders known from the Upper Carboniferous persisted into the Permian, some with significant changes in diversity (Fig. 1.06, 1.07). This has been attributed to the continued rise of herbivory following the advent of the gymnosperms (Jarzembowski and Ross 1993; Gullan and Cranston 1994). The Ephemeroptera, which diversified greatly, are represented in the fossil record by both nymphs and adults (Carpenter 1979). The adults had well-developed mandibles, in contrast to extant mayflies in which the mouth parts are atrophied and non-functional. The nymphs were similar to those of modern species. The diversity of the Palaodictyoptera decreased markedly in the Permian. In some species the hind wings were reduced or completely lost. Both the Megascoptera and the Diaphanopterodea became much more diverse; the latter are considered the most highly specialised of the Palaeoptera (Labandeira and Sepkoski 1993). The Protodonata changed little in diversity or morphology. The Protorthoptera reached their peak in this period (Labandeira and Sepkoski 1993). Blattodea were considerably less abundant, almost certainly due to a

loss of suitable habitat (Wootton 1981). The Orthoptera, Caloneurodea and Miomoptera became extremely abundant.

The orders Odonata (dragonflies and damselflies), Plecoptera (stoneflies), Protelytroptera (extinct forms similar to beetles, but with affinities to earwigs and protorthopterans), Psocoptera (bark lice), Thysanoptera (thrips) and Hemiptera (true bugs) appear in the Permian (Fig. 1.02, 1.07). Among the endopterygote neopterans to appear were the Mecoptera (scorpionflies), Neuroptera (alderflies, snake flies and lacewings), Trichoptera, the extinct Glosselytrodea, and perhaps most importantly, the Coleoptera.

MESOZOIC ERA

Triassic

The Triassic is one of the poorest known periods in the evolutionary history of insects (Carpenter and Burham 1985; Fraser *et al.* 1996). There is a marked decline in familial diversity (Fig. 1.06) (Labandeira and Sepkoski 1993), which has been interpreted as reflecting the terminal Permian mass extinction (Labandeira and Sepkoski 1993; Jarzembowski and Ross 1993). However, recent discoveries of Triassic representatives of seven living families/orders in the Solite Quarry of Virginia, U.S.A. suggests that this minimum is a sampling artefact attributable to the paucity of insect deposits (Fraser *et al.* 1996). Apart from the Virginian deposit, the Issyk-Kul site of Kirgizia and the amber of Lebanon (Zur Strassen 1973) are the most important Triassic sites of the northern hemisphere (Table 1.2). The principal sites of the southern hemisphere are Mount Crosby and Denmark Hill in south-eastern Queensland, and Brookvale in N.S.W., Australia; (Riek 1970; see Chapter 7) (Table 1.2). Insects from the Molteno 'Formation' of South Africa (Riek 1974) may also prove important but await detailed study.

Eight orders did not survive the end Permian, suggesting a major extinction event (see Fig. 1.06, 1.07). Groups which did survive continued to diversify during the Triassic, particularly the Ephemeroptera, Odonata and most of the exopterygote Neoptera (Pritykina 1981). The order Phasmida (walking sticks) made its first appearance (Rohdendorf 1962), as did the Diptera (true flies) (Rohdendorf 1964) and Hymenoptera (bees and wasps) (Rasnitsyn 1964, 1969, 1975).

Jurassic

The insect faunas of the Jurassic are better known than those of the periods that precede and follow it due to the extensive insect-bearing localities of the former Soviet Union (Carpenter and Burnham 1985) (Table 1.2), particularly Karatau, Kazakhstan and Turkestan. Other significant deposits include those of the English Lias and the renowned Solnhofen Limestone of Germany (Table 1.2).

Many living families appeared during this period, although extinct families still generally predominate (Carpenter and Burnham 1985). The order Dermaptera (earwigs) was the only new order to appear in the Jurassic. The fossils resemble the living species in general appearance but differ in having cerci that are long and multi-segmented (Vishniakova 1980).

Cretaceous

The majority of Cretaceous insects belong to extant families and the fauna of this period is therefore essentially modern (Carpenter and Burnham 1985). The precipitate rise of insect diversity during this period has been attributed by some workers to the diversification of angiosperms which first appeared in the Lower Cretaceous (Strong *et al.* 1984). However, Labandeira and Sepkoski (1993) demonstrated that the rate of increase of insect diversity actually slowed during angiosperm radiation. The post-Palaeozoic radiation of insect families began more than 100 million years before the appearance of angiosperms. The insect orders that radiated strongly during the Mesozoic and Cenozoic, such as Coleoptera, Diptera and Hymenoptera, all began to expand during the Triassic and Jurassic (Fig. 1.07). This suggests that the radiation of the insects may have driven the rapid expansion of angiosperms during the mid-Cretaceous, rather than vice versa.

A number of significant Cretaceous insect faunas have been described within the last twenty years (listed here from oldest to youngest) (see Table 1.2 which includes references): the Wealden and Purbeck of England; Montsech, Spain; the Jiuquan Basin, Gansu, China (Hong 1982); the Koonwarra Beds of Victoria, Australia (see Chapter 7); the Crato Member, Santana, Brazil; and the ?volcanic crater of Orapa, Botswana (McKay and Rayner 1986; Kuschel *et al.* 1994). In addition, insects are being described from several Cretaceous ambers, principally from Lebanon, France, Siberia, New Jersey, Alberta and Manitoba (Poinar 1992; Grimaldi 1995).

The Cretaceous marked the appearance of social insects (Burnham 1978). Both workers and reproductive ants have been described from the amber of New Jersey and Siberia suggesting at least some form of social organization (Burnham 1978).

Two orders appeared, the Isoptera (termites), which may also have been social (Jarzembowski 1981), and the Lepidoptera (butterflies and moths) (Skalski 1979), the appearance and radiation of which of which undoubtedly correlates with the origin of the angiosperms (Labandeira and Sepkoski 1993).

CENOZOIC ERA

Tertiary

After the demise of the 'ancient' groups, around half the orders that survive to the Recent underwent modest to spectacular diversification during the Tertiary, in most cases continuing to the present (Gullan and Cranston 1994). The Tertiary insect fauna

Table 1.2 Principal insect-bearing lagerstätten of the world. (See end of table for key).

	Deposit	Age	Location	Depositional environment	Preservation		Taxa	Authors
					Style	Completeness		
	Rhynie	Pragian	E. Scotland	Lacustrine	Silicification	Complete specimens	Collembola	Whalley & Jarzembowski 1986; Rice & Trewin 1986; Trewin 1989
	Hagen-Vorhalle	Namurian	W. Germany	Limnic basin	Coalification	Complete specimens	Palaeodicty, Mega, Odon, Protor	Brauckmann *et al.* 1985 Brauckmann 1988, 1989
	Saar	Westphalian B	W. Germany	Limnic basin	Coalification	Wings	Blatt, Palaeodicty, Protor, Protod	Gunthörl 1934, 1963 Waterlot 1934a,b
	Writhlington*†	Westphalian D	S.W. England	Deltaic	Coalification	Wings, also nymphs & body parts	Blatt, Protor, Palaeodicty	Jarzembowski 1987, 1989, 1994 (& references therein)
	Kuznetsk Basin	Westphalian/ Stephanian	Siberia, C.I.S.	Limnic basin	Coalification	Wings	Blatt, Palaeodicty, Protor, Protod, Odon	Rohdendorf 1957b, 1958, Rohdendorf *et al.* 1961
	Mazon Creek°	Westphalian D	Illinois, U.S.A.	Deltaic	Siderite concretions	Complete specimens	Blatt, Protor, Palaeodicty, Odon	Richardson 1956, Carpenter & Ricardson 1971, Baird *et al.* 1985a, b
	Commentry	Stephanian	France	Limnic basin	Siderite concretions	Wings	Protodo, Mega, Calon, Palaeodicty Blatt, Protor	Lameere 1917; Carpenter 1943a, 1964b Kukalová 1970
	Boskovice Trough	Sakmarian	Moravia, Crech Rep.	Limnic basin	Coalification	Wings	Mega, Palaeodicty, Protor, Col, Miom, Protelytoptera	Kukalová 1963, 1965, Kukalová-Peck 1975

* See Chapter 3.

° See Chapter 4.

† For a review of the insects of the British Coal Measures, see Bolton (1921-22) and North (1931).

	Deposit	Age	Location	Depositional environment	Preservation		Taxa	Authors
					Style	Completeness		
	Elmo*	Artinskian	Kansas, U.S.A	Saline lake/ lagoon	Coalification	Wings	Mec, Blatt, Protod Palaeodicty, Odon, Hem, Neur, Protor Orth	Tillyard 1937 Carpenter 1930, 1964a, 1966
	Tshekarda	Kungurian	Urals, C.I.S.	Riverine/l acustrine	Coalification	Wings, some larvae & body fragments	Mega, Col, Hem, Blatt, Protelytoptera	Rohdendorf 1939, 1940, 1944, 1957
	Kuznetsk Basin	Kungurian	Siberia, C.I.S.	Lacustrine	N/A	Wings, body fragments	Hom, Meco, Col	Rohdendorf 1958 Rohdendorf *et al.* 1961
	Belmont & Warner's Bay	Tartarian	N.S.W. Australia	Lacustrine	Calcitic replacment in chert	Wings	Hom, Psoc, Mec, Neur, Col	Knight 1950, Reik 1968, 1970a, b
	Solite Quarry	Carnian	Virginia, U.S.A.	Meromictic lake	alumino-silicate films	Intact	Hem, Blatt, Col, Dip, Orth, Trich, Thys,	Fraser *et al.* 1996
	Mt. Crosby/ Denmark Hill	Rhaetic	Queensland Australia	Deltaic	Coalification	Wings	Blatt, Hom, Col	Tillyard 1916, Tindale 1945 Reik 1955, 1956
	Issyk-Kul	Triassic	Tien Shen Mts, Kirgizia	Lacustrine	Impressions	Wings	Dip, Mec, Hom	Rohdendorf 1957, 1961, 1962, 1964

* At its greatest extent, the saline lake covered Oklahoma, Nebraska and Colorado (Carpenter 1945; Tasch & Zimmerman (1962).

	Deposit	Age	Location	Depositional environment	Preservation		Taxa	Authors
					Style	Completeness		
	Charmouth Cliff	Sinemurian	Dorset, S.W. England	Marine	Impressions, some original cuticle	Wings, some paired. Some intact specimens	Col, Orth, Het, Hom, Mec, Odon, Blatt	Zeuner 1939, 1962 Whalley 1985
	Karatau	Malm	Kazakhstan	Lacustrine	Impressions	Wings	Eph, Dip, Raph, Neur, Mec, Col	Rohdendorf 1947, 1957, 1962 Demoulin 1956 Arnoldi 1977
	Southern Turkestan	Malm	Turkestan	Lacustrine	N/A	Wings	Col, Orth, Hom, Mec, Hym, Phas, Odon, Thysan, Psocop, Raphid	Martynov 1925a, b, c, d
	Solnhofen	Tithonian	W. Germany	Restricted marine/lagoon	Impressions (plattenkalk)	Intact outlines (only winged specimens)	Blatt, Odon, Orth, Ephem, Phas,Col, Neur, Hem, Dip, Trich, Hym	Carpenter 1932 Barthel *et al.* 1990
	Purbeck	Berriasian	Dorset, S.W. England	Lacustrine	?Altered organics	Wings, also intact individuals	Col, Orth, Odon, Blatt, Dip, Hem, Trich, Phas, Hym, Neur, Raph	Allen & Wimbledon 1991 Jarzembowski 1992
	Montsech	Barriasian/ Valanginian	S.E. Spain	Peritidal/ lacustrine	Impressions ?cuticle traces (plattenkalk)	Wings, intact outlines	Col, Eph, Blatt, Hem, Dip, Hym	Whalley & Jarzembowksi 1985 Martinéz- Delclós *et al.* 1991a Martinéz- Delclós & Martinell 1993

	Deposit	Age	Location	Depositional environment	Preservation		Taxa	Authors
					Style	Completeness		
	Weald*	Barremian/ Hauterivian	S.E. England	Lacustrine/ lagoonal/mud plain	Calcification/ phosphatiz-ation	Wings	Col, Blat, Orth, Het/Hom, Hym Odon, Mec, Iso, Trich	Jarzembowski 1991a, b Ross & Cook 1995 Cook & Ross 1996
	Crato, Santana	Aptian	N.E. Brazil	Lacustrine	Goethite°, mineral replacement (plattenkalk)	Intact specimens	Eph, Od, Derm, Dip, Iso, Col, Derm, Het/Hom, Hym	Grimaldi 1990 Maisey 1991
	Koonwarra	Aptian	Victoria, Australia	Lacustrine	Calcification	Intact specimens	Het/Hom, Col, Dip, Blatt, Plec, Orth, Psoc, Mec & immature Eph, Od	Jell & Duncan 1986
	North America♠	Palaeogene						
	Mo-Clay	E. Eocene	Denmark	Marine	Calcification, concretions in ash	Intact - only winged individuals	Het, Col, Hom, Orth, Neur, Dip, Hym	Larsson 1975 Willman 1990
	Geiseltal	M. Eocene	E. Germany	Lacustrine	Altered organics	Intact specimens	Coleoptera	Voight 1988 Koenigswald 1989

* See Chapter 5.

° The freshly excavated specimens are pyritic. Goethite is the weathering product (Wilby *pers. comm.*).

♠ For a full review and discussion, see Chapter 6.

	Deposit	Age	Location	Depositional environment	Preservation		Taxa	Authors
					Style	Completeness		
	Messel	M. Eocene	W. Germany	Lacustrine	Altered organics	Intact specimens	Col, Hym, Het	Schaal & Zeigler 1988 Lutz 1990, Franzen 1990
	London Clay	Eocene	England	Marine	Pyritization	Bodies often missing appendages	Coleoptera, Hemiptera	Britton 1960, Rundle & Cooper 1971, Allison 1988b, Jarzembowski 1992
	Bembridge*	L. Eocene/ Oligocene	Isle of Wight, England	Lagoonal	Altered organics & calcification	Wings, intact specimens	see Chapter 7	Daley 1969, 1972, 1973 Jarzembowski 1980 McCobb *et al.* 1997
	Baltic amber†	L. Eocene/ E. Oligocene	Baltic, N.W. Europe	Amber	Altered and original organics	Intact specimens	All modern insect taxa	Dietrich 1975, Larsson 1978, Schlüter 1990
	Rott	L. Oligocene/ Miocene	W. Germany	Lacustrine	Altered organics	Wings, intact specimens	Het, Dip, Col, Odon	Lutz 1989 Koenigswald 1989
	Dominican amber†	Dominican Republic	Carribean	Amber	Altered and original organics	Intact specimens	All modern insect taxa	Henwood 1992, 1993, Grimaldi et al 1994, Grimaldi 1995
	Riversleigh*	Miocene	Queensland, Australia	Lacustrine	Phosphatiz-ation	Intact specimens, inc. larvae	Col, Trich, Hym	Archer *et al.* 1989, 1991 Duncan & Briggs 1996 Duncan *et al.* 1997
	Rusinga	Miocene	Lake Victoria Kenya	Volcanic ashfall	Calcificaion	Bodies, often missing appendages	Blatt, Orth, Col, Hym, Lep	Leakey 1953, 1963, Lees 1953

* See Chapter 7.

† For a review of these amber deposits and others, see Poinar (1992), and Grimaldi (1996).

	Deposit	Age	Location	Depositional environment	Preservation		Taxa	Authors
					Style	Completeness		
	Clarkia°	M. Miocene	Idaho, U.S.A.	Lacustrine	Altered organics	Intact specimens	Col, Dip, Hym	Smiley *et al.* 1975 Smiley 1985 Lewis 1985
	Oeningen	Miocene	W. Germany	Lacustrine	N/A	Wings, rare intact specimens	Col, Hem, Hym, Dip, Neur, Orth, Lep	Jörg 1966, Westphal 1978 Scudder 1895a
	Barstow	M.-L. Miocene	California, U.S.A.	Lacustrine	3D replacement in suite of minerals	Intact	Col, Dip, Hym, inc. larvae	Palmer 1957, Park 1990, 1995
	Rancho La Brea*	Pleistocene	California, U.S.A.	Asphalt	3D original cuticle	Intact	Col, Dip, Hym, Blatt, Odon	Akerstein *et al.* 1983 Miller 1983, Stock 1991
	Peat†	Quaternary						

° For a full review of North American Neogene insect faunas, see Lewis & Heikes (1991).

* See Chapter 8.

† For a detailed reveiw of peat deposits, see Elias (1994).

CARBONIFEROUS
PERMIAN
TRIASSIC
JURASSIC
CRETACEOUS
TERTIARY
QUATERNARY

Table 1.2 Principal insect-bearing lagerstätten of the world. Full names of the abbreviated taxa can be found in Figure 1.02. Underlined authors represent principal reference.

is essentially modern. The apparent sharp rise of diversity evident in Figure 1.06 is an artifact, reflecting an abundance of insect lagerstätten (Labandeira and Sepkoski 1993). It is expected that, as older ambers and compression fossils are studied, this peak will be pushed back from the mid-Tertiary into the late-Mesozoic.

Although Tertiary fossil insects are particularly abundant and accessible, their recorded generic and even family identifications are not always reliable (Carpenter 1992). Many were named a century or more ago and placed in existing genera, long before current concepts of those genera were reached (Carpenter 1992, p. 13).

The largest insect-bearing deposits of the Tertiary are those of North America (see Chapter 5; Fig. 5.03). However, perhaps the most important faunas occur in amber, particularly Dominican (Poiner 1992; Grimaldi 1995) and Baltic (Larsson 1978; Schlüter 1990; Langenheim 1990), from which the earliest records of many extant families derive. However, the sampling bias inherent in amber must be recognized (see Henwood 1992, 1993). Other significant deposits are detailed in Table 1.2 and include the German oil shales of Messel and the compression fossils of Rott and Oeningen; the compression fossils of the Mo-Clay, Denmark; the 3D phosphatized insects of Riversleigh, Australia (see Chapter 7) and Quercy, France (Handschlin 1944); and the 3D organic-replaced insects of the Bembridge Marls, Isle of Wight, England (see Chapter 7). The pyritized insects of the London Clay, and the calcified insects of Rusinga, Lake Victoria, Kenya, may be significant, but await detailed study.

Nearly all of the Tertiary families have living representatives (Carpenter and Burnham 1985). Five new orders appear; Zygentoma (silverfish), Manteodea (mantids), Embioptera (web spinners), Siphonaptera (fleas) and Strepsiptera (Fig. 1.02, 1.07).

Quaternary

The Quaternary fauna is modern. Coope (1978, 1979) and Matthews (1970, 1976) were able to place all fossil beetles from Pliocene and Pleistocene lake deposits in Britain and northern Canada into modern species on the basis of characters of the genitalia; assignment was possible despite profound changes in the biogeographic distributions of the descendant populations. Despite claims for significant extinctions attributed to various Ice Ages (*e.g.* Pierce 1946), recent revisions have demonstrated that their importance was minor (Elias 1994). The primary deposits are temporary in nature, in that decay re-commences upon the removal of the insect from the preservational medium. Most of the diversity of Quaternary insects is recorded from the various peat deposits around the world (see Elias 1994). Asphalt deposits, such as Rancho La Brea and McKittrick, California, U.S.A. (Table 1.2; Chapter 8), while more limited in extent, also provide valuable information (Miller 1983).

1.6 AIMS AND SCOPE OF WORK

The aim of this project was to examine and quantify the conditions that control insect taphonomy. The subject of insect taphonomy, though rarely discussed, is of particular importance. Insects have invaded almost every ecological niche. They are the most commonly preserved terrestrial fossil. A greater understanding of their decay and preservation will have implications beyond the taxonomic boundary of the class. These aims of the project were fulfilled through a series of actualistic experiments and case studies of selected lagerstätten.

Actualistic experiments were designed to quantify the rate of decay and the effect of transportation upon the insect. CHAPTER 2 examines the influence of morphotype upon decay under laboratory and natural conditions. The breakdown of the various insect orders is documented in an attempt to find a general decay sequence. Decay is also studied at a microscopic level with the disintegration of cuticle recorded and related to the biochemical breakdown of the constituents of insect cuticle. CHAPTER 3 tests the effect of decay and transport on the skeletal durability of the cockroach. These results are used to interpret the taphonomy of a Carboniferous lagerstätten (see below). The results of the various insect experiments are used to gain an insight into the taphonomy of various lagerstätten.

Insects are generally fossilised in one of four broad preservational styles:- organic, authigenic mineralisation, nodular or impressions.

1. Organic preservation. Organic material can be preserved largely unaltered, the tissue retaining original biogeochemical signatures, or altered to a more recalcitrant material. Most Quaternary insects preserve the original organic chemistry (Elias 1994). Although much taxonomic work has been conducted upon these fossils (see Elias 1994), little research has been conducted upon of their biogeochemistry. CHAPTER 8 considers the biogeochemistry and structural preservation of the insects of the asphalt seeps of Rancho La Brea, California, U.S.A..

Insects embedded within amber are perhaps the most familiar of insect fossils. Although it has been alleged that these fossils retain original biochemical signatures, including DNA traces (Cano *et al.* 1992, 1993; DeSalle and Grimaldi 1994), recent study has cast doubt upon the validity of these claims (Smith *et al.* 1997) Amber deposits are relatively common and vary greatly in age and botanical origin (Langenheim 1968; Rice 1987; Poinar 1992). To date Dominican (Baroni-Urbani and Saunders 1982; Grimaldi 1995) and Baltic (Larsson 1978) amber have received the most attention. However, older ambers are now being studied in an attempt to resolve some of the questions regarding early insect diversification (Carpenter and Burnham 1985). Since the taphonomy of amber insects has been the subject of a recent study (Henwood 1992, 1993) a case study is omitted.

Organic material can also be preserved highly altered. Replication of detail is no guarantee of unaltered chemistry. CHAPTER 7.3 considers the insects of the Bembridge Marls, Isle of Wight, where the organically preserved cuticle displays a remarkable structural fidelity. The insects of the Green River Formation, Piceance Creek Basin, Colorado discussed in CHAPTER 6 are also organically preserved and display a remarkable fidelity in hand specimen. These chapters document the geology of the respective lagerstätten, and analyse the biogeochemistry of the insects to understand the behaviour of organic biomolecules in the rock record.

Insects may be organically preserved through a coalification process, whereby all structural detail save the outline of the from of the particular insect is lost. Insects are commonly recovered from the Carboniferous Coal Measures. The insects of these deposits are predominantly represented by wings alone. CHAPTER 3 examines the taphonomy of one of one such deposit, Writhlington, and uses the findings of a series of actualistic experiments to interpret the results.

2. *Authigenic mineralisation.* The formation of authigenic minerals often produces fossils of remarkable fidelity. The most important minerals are apatite (calcium phosphate), calcite (calcium carbonate) and pyrite. Apatite is a particularly important source of palaeontological data, frequently preserving extraordinary detail (*e.g.* Martill 1990). The precipitation of apatite or calcite has been compared to a 'switch', with the default set for the precipitation of $CaCO_3$ (Allison 1988; Briggs and Wilby 1996). Phosphatized biotas have received much attention in the last decade (see Martill 1988, 1989; Schultze 1989; Wilby 1993; Briggs *et al.* 1993; Martill and Wilby 1994; Wilby and Whyte 1995; Wilby *et al.* 1995), with the processes of phosphatization successfully induced in the laboratory (Briggs and Kear 1993b, 1994b). CHAPTER 7.2 examines the remarkable phosphatized insects of Riversleigh, Queensland, Australia, with reference to the various preservational fabrics and what they reveal about the timing of fossilization.

The experiments of Briggs and Kear (1993b, 1994b) reveal that the position of the 'switch' is dynamic, with early phosphate often overgrown with calcite as the pH rises. CHAPTER 5 discusses the insects of the Weald, S.E. England where both apatite and calcite are found intimately related. The chapter discusses the various mineral fabrics and assesses their implication for the timing of fossilization. A similar relationship is to be found in the nodules of the Mazon Creek, Illinois, U.S.A which are discussed in CHAPTER 2 (see below).

The process of pyritization has perhaps attracted the greatest interest (*e.g.* Berner 1970, 1971, 1985; Lein 1978; Curtis 1980). Pyritized insects are reported from the London Clay of England (Rundle and Cooper 1970; Allison 1988a) and the Crato Member of the Santana Formation, Brazil (Grimaldi 1990). The insects of the latter

deposit are currently the subject of a study by D.M. Martill of the University of Portsmouth. Consequently, a case study of pyritization is omitted.

3. Nodular. Insects preserved in nodules are recorded from a number of localities (Table 1.2). Notable examples include those of Mazon Creek, Illinois, U.S.A (Richardson 1956; Nitecki 1979) and Montceau-les-Mines, France (Heyler 1980) (see Baird *et al.* 1985a for a review). CHAPTER 4 examines the mineralized insects of Mazon Creek, Illinois in an attempt to understand the processes of mineralization and the timing of nodule formation. Insects preserved in iron nodules are also noted in the Piceance Creek Basin of Colorado (CHAPTER 6). These nodules are found at a similar stratigraphic level to the insects which are organically preserved, allowing comparison of the two styles of preservation and facilitating an understanding of the timing of nodule formation.

Calcitic nodules are recorded from a number of localities *e.g.* Barstow, California, U.S.A (Palmer 1957; Park 1990) and Mo-Clay, Denmark (Larsson 1975; Willmann 1990) (Table 1.2). Calcitic nodule formation is currently being studied by Lisa E. Park of the University of Arizona (see Park 1995). A study of this form of preservation is therefore omitted, although the mode of fossilization is reviewed in CHAPTER 7.

4. Impressions. Insects preserved simply as impressions are not uncommon, even in deposits where other preservational styles predominate. It appears that impressions are the end product or relics of an earlier taphonomic sequence (Tischlinger 1996). Consequently this phenomenon is not treated separately.

CHAPTER 2

ACTUALISTIC EXPERIMENTS: DECAY

2.1 INTRODUCTION

Rate of decay is a critical factor in the preservation of fossils. However, the measurement of rate - decay per unit time - is not straightforward. Fortunately invertebrates tend to decay through the same gross sequence of morphological stages regardless of circumstance (see Briggs and Kear 1993a). These stages provide a coarse measure of decay, with the added advantage that they can be related directly to fossils (*e.g.* Briggs and Kear 1993a,b, 1994a).

2.2 PREVIOUS WORK

2.2.1 Introduction

The application of the Lyellian dictum, the present is the key to the past, has a long tradition in palaeontology: *e.g.* observational palaeontology (aktuopälaontologie), where body and trace fossils and are interpreted by comparison with present day organisms and their traces (Schäfer 1962, 1972). However, experimentation, as opposed to observation, has a more recent pedigree (see Behrensmeyer and Kidwell 1985; Briggs 1996, for a review).

A great deal can be learned about the processes of fossilization through experiment. Many recent advances reflect an appreciation of the central role played by organic decay. By simplifying conditions and exploring the influence of changing variables, such as oxygen level, temperature, salinity and microbial action, the important factors controlling decay (and its inhibition), disarticulation and fossilization can be investigated and their role determined. Documentation of the decay stage is essential to the interpretation of similar fossil taxa. The popular notion that soft-bodied fossils are pristine representations of past life is generally false. Decay has usually commenced, and may be well advanced before fossilization begins. Interpretation is therefore dependent upon comparing the product of actualistic decay experiments with the fossil, *i.e.* like with like. Decay experiments allow the preservation potential of taxa to be investigated and quantified

2.2.2 General

Many experiments have been conducted upon biomineralized hard parts (*e.g.* vertebrate assemblages: Behrensmeyer 1975, 1982, Zangerl 1971; echinoids: Kidwell and Baumiller 1990, Allison 1990, Greenstein 1991; bivalves and brachiopods: Allen 1984, Alexander 1984, Glover and Kidwell 1993, Lutz *et al.* 1994; foraminiferans: Kotler *et al.* 1992; see Behrensmeyer and Kidwell 1985 for review). Plant taphonomy has also received considerable attention (see Spicer 1991) and is currently under experimental investigation by Margaret E. Collinson of the University of London (Royal Holloway). This section reviews actualistic experiments pertinent to the decay of non-mineralized animal tissue.

Early experiments conducted by Plotnick (1986) investigated the decay of shrimps (*Pandulus*) both in the field and open jars in the laboratory, with and without sediment. The shrimps were killed by freezing and the experiments run at 12°C. The results were recorded at intervals of 1, 3, 7, 21 and 28 days, by which time the shrimps were reduced to numerous tiny cuticle fragments. Observations were qualitative and based on monitoring changes in individual specimens throughout the duration of the experiments; weight loss was not measured. Plotnick (p. 209) concluded that decay was "somewhat faster in the open jars" but that no difference was evident after two weeks, and that "decomposition appeared to be only slightly faster when sediment was present" (p. 209).

Allison (1988a) also investigated the decay of shrimps (*Nephrops*, and *Palaemon*) as well as polychaetes (*Nereis).* The carcasses were placed in jars containing sediment and water from marine, brackish and lacustrine environments, at room temperature. The experiments were terminated and the jars sampled at intervals of 2, 6, 12, 18, and 25 weeks. Allison concluded that anaerobic decay was rapid, virtually destroying shrimp carcasses in 25 weeks, and that anoxia was therefore ineffective as a long term conservation agent of soft-bodied fossils.

Both Plotnick and Allison produced qualitative results. Subsequently Briggs and Kear introduced greater quantification in a series of experiments conducted on a range of taxa between 1992 and 1994.

The initial experiments of Briggs and Kear (1994a) sought to investigate degradation of the polychaete *Nereis* under a variety of conditions (20°C, artificial sea water: rapid diffusion of oxygen, slow diffusion, slow diffusion with de-oxygenated water, no diffusion and complete anoxia). Decay was monitored in terms of morphological change, weight loss and change in chemical composition.

The experiments revealed five stages of decay: whole/shrivelled, flaccid, unsupported gut, cuticle sac, jaws and setae. Initial degradation (<3 days) affected mainly the lipids and collagen of the cuticle. Continued decay degraded proteins, so increasing the relative proportion of refractory structural components (sclerotized chitin and collagen). Thus without early mineralization only sclerotized tissue is likely to survive. A number of other conclusions were reached: complete elimination of oxygen significantly reduces the decay

rate of volatiles; oxygen diffusion influences the osmotic uptake of water by the carcass and affects water pH; in the absence of bacteria, full degradation of the carcass is impossible; where carcasses are introduced into sterile water, the bacteria of the gut are sufficient to initiate decay.

The experimental protocol of these first experiments was maintained during investigation of the decay and early mineralization of shrimps (*Crangon*) and prawns (*Palaemon*) (Briggs and Kear 1994b). The influence of initial oxygen level, and closure of the system to oxygen diffusion, were investigated, while weight loss, change in morphology and chemical composition, and mineral formation were documented. Decay resulted in five morphological stages: swollen (due to osmotic uptake), ruptured (as the exoskeleton split), hollow (as the muscles shrunk), disarticulated (as elements of the exoskeleton separate), and finally fragmented. The availability of oxygen did not strongly influence decay rate (as measured by weight loss).

The next experiment of Briggs and Kear (1994a) sought to resolve the 'conodont problem' (for discussion, see Rhodes 1954; Hass *et al.* 1962; Lindstrom 1964; and Brasier 1992). Conodont body fossils display a number of problematic features impossible to resolve using fossil evidence alone (Aldridge *et al.* 1993; Briggs and Kear 1994a; Gabbott *et al.* 1995): Are the paired axial lines running the length of the trunk, gut margins or notochord? Is the displaced position of the 'element apparatus' real, due to the loss of supporting tissue, or a taphonomic artifact? What is the nature of the V-shaped, non-contiguous, structures running the length of the trunk?

Decaying the cephalochordate *Branchiostoma*, arguably the closest living analogue to the conodont animal, Briggs and Kear (1994a) noted that the myomeres and notochord, often the animal's most ventrally preserved features, are quickly exposed by decay of the surrounding skin. Similar decay in conodonts would explain the apparent lack of supporting tissue around the apparatus, while the elements retain a constant position relative to body. The notochord sheath of *Branchiostoma* is particularly recalcitrant, allowing the parallel lines within the trunk of the conodont to be interpreted as the margins of the notochord, rather than the more labile gut wall. As the muscles of *Branchiostoma* decay, so the myomeres within shrink, explaining the discrete preservation of the V's along the conodont animal trunk.

Briggs and Kear conducted a series of preliminary decay experiments on shrimps (Baas *et al.* 1995) and *Rhabdopleura* (Briggs *et al.* 1995) in an attempt to explain why the composition of cuticle/periderm recovered from the fossil record cannot be explained readily as a decay product of their living equivalents. Fossils investigated using pyrolysis-GC/MS yield two distinct chemical signatures, dominated either by straight chain aliphatics or by aromatic compounds, neither of which can be directly related to modern biomolecules from similar tissue. On-going experiments conducted on a range of arthropod taxa (shrimp, cricket, beetle, scorpion, millipede) have attempted to quantify this phenomenon further (Stankiewicz *et al.* 1996, 1997a, b, c; Chapter 8).

2.2.3 Insect-specific

Few experiments have been carried out to investigate insect taphonomy. To date, detailed experiments have been conducted only on the orders Diptera (Henwood 1992) and Blattodea (Lutz 1992). Observational experiments on the buoyancy properties of a range of orders were carried out by Martínez-Delclòs and Martinell (1993), but their protocol was less rigorous. General observations on insect decay were recorded by Seastedt and Tate (1981), Seastedt and Crossley (1984) and Okafer (1966).

Henwood (1992) investigated amber preservation by focusing on the flight muscle of the dipteran *Calliphora vomitoria*. Through comparison of the tissue of amber insects and modern correlates, she deduced that dehydration was primarily responsible for the remarkable preservation. Flies were treated in three different ways: suspended above a dehydrating agent in an airtight desiccator, embedded in (air/water impermeable) paraffin wax, and immersed in maple syrup (an analogue of amber resin). Control specimens were maintained in empty, sealed glass vials.

The flies were killed with chloroform (which may mimic amber resin's bacteriocide properties: Henwood 1993). The experiments were maintained at 23±3°C away from natural light. Sampling intervals ranged from 12 hours to 30 days. The tissue was extracted, fixed and sectioned for TEM examination. Decay was monitored on the basis of morphological changes to the muscle tissue, and quantified using the shrinkage of the flight muscle (by counting the number of myofibril cross sections per unit area). The flies embedded in syrup showed the greatest similarity to those preserved in amber. Henwood deduced dehydration as the major factor in the preservation of the muscle tissue. However, Grimaldi *et al.* (1994, p. 10) observed no shrinkage of internal tissues in their study of Dominican amber flies. It therefore appears that dehydration may be important in certain cases, but is not universally so.

Lutz (1984, 1990) conducted a series of decay experiments upon a range of insect orders (Blattodea, Orthoptera, Coleoptera, Hymenoptera and Diptera) under laboratory and lake conditions in order to interpret the preservation of the Tertiary insects of Grube Messel. The experimental conditions were not specified (Lutz 1990). However, there are some data on experiments on the cockroach (Lutz 1984) (pond temperature ~25°C; 10 specimens). Lutz also recorded a general sequence of decay (Fig. 2.01).

Lutz (1990) stated that it is impossible to produce quantifiable results due to the great variation in decay, even between individuals of the same species. He attributed this variation both to individual factors, *e.g.* body fat/stomach content, or behaviour on the water surface, and to external factors, *e.g.* water temperature, the activity of wind, currents and rainfall. However, no evidence was given to support these assumptions. Neither was any information on specimen numbers provided, so the validity of the statements remains uncertain.

Lutz (1984) used his experimental work on the cockroach to demonstrate that an insect family from the Grube Messel of Germany, known only from its wings, is invalid. He

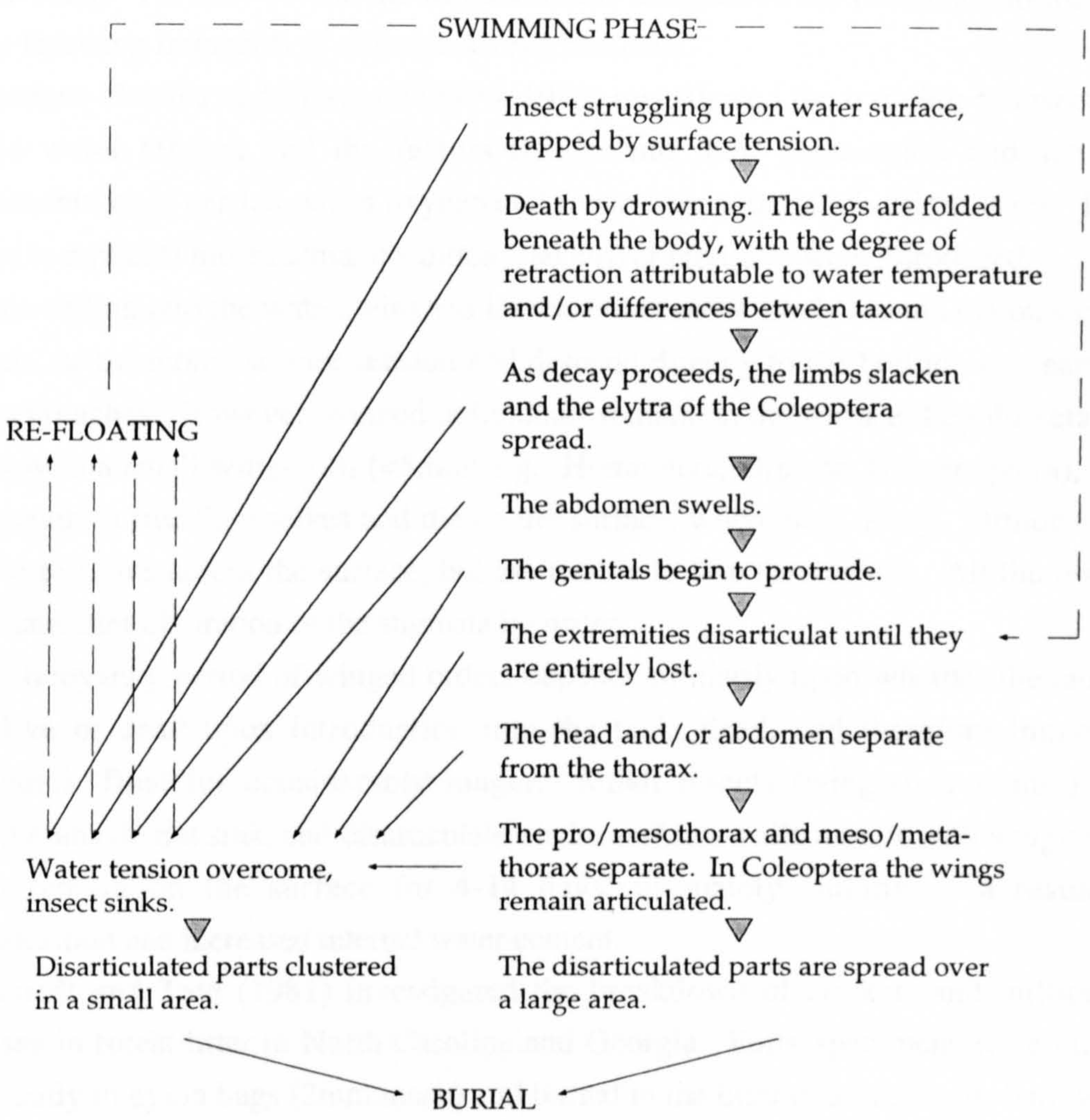


Figure 2.01 Schematic representation of the results of the actualistic experiments of Lutz (1990).

noted that the clavus (anal area) of the tegmina that separates during decay of the cockroach bore a striking resemblance to the tegmina of the family Parallelophoridae (Haupt 1956). He showed that the Messel fossils assigned to the Parallelophoridae are simply forewing fragments of other cockroach families.

Martínez-Delclòs and Martinell (1990, 1993) investigated the trapping of insects by surface water tension and the factors that permit their submersion and settling. Experiments were carried out in oxygenated freshwater aquaria of various sizes. In an attempt to replicate more natural conditions, lake/river predators were introduced.

Upon falling into the water, wingless insects either move freely around the on surface *e.g.* ants, or overcome surface tension and descend directly to the bottom, *e.g.* earwigs and cockroaches. However, winged individuals remain on the surface. Lepidoptera and insects with a small wing-span (<5mm; *e.g.* Homoptera, Diptera, Hymenoptera), lack the strength to free themselves and die on the surface, where they decay. Orthopterans are able to move across the surface, but are unable to free themselves. All the insects asphyxiate after obturation of the stigmata by water.

The buoyancy period of winged orders depends primarily upon whether the animal was alive or dead upon introduction into the tank; dead, and therefore immobile individuals, float for considerably longer. Small insects (wing-span <5mm) and lepidopterans do not sink, and disarticulate on the surface, while insects with wing-spans >5mm remain on the surface for 4-14 days, ultimately sinking as a result of decomposition and increased internal water content.

Seastedt and Tate (1981) investigated the breakdown of cricket (and millipede) carcasses in forest litter in North Carolina and Georgia. Forty specimens were placed individually in nylon bags (2mm mesh) and buried in the litter of a deciduous hardwood forest. Four bags were sampled weekly for the first two months, and at more widely separated intervals thereafter. The focus of the experiments was to detail mass and nutrient loss, and to measure the abundance of micro-arthropods on the cricket remains (Seastedt and Crossley 1984). The remains decomposed slowly; five years was estimated as the time necessary for complete disappearance of millipede and cricket exoskeletons. Soft tissue, however, apparently disappeared within the first two weeks (see also Seastedt and Crossley 1984). Spiders, centipedes and other invertebrate and vertebrate scavengers, reduced the carcass to exoskeletal remains, either as unconsumed portions of wings, legs and other fragments, or as chitinous fragments in faeces.

Okafer (1966b) studied the decomposition of insect remains in a terrestrial environment. He did not measure mass loss, but found recognisable fragments of desert-locust wings after 300 days.

The insect experiments to date have focused on particular taphonomic problems. Henwood's (1992) experiments relate only to insects in amber. The less rigorous studies of Lutz (1984; 1990) have particular relevance only to the insects of the Grubbe Messel, and suffer from a poorly defined and iterated protocol. Although Lutz (1990) did

produce a summary diagram of the stages of insect decay, it is so general as to be of little value. The work of Martínez-Delclòs and Martinell (1990, 1993) is primarily observational. The experiments of Okafer (1966b), Seastedt and Tate (1981) and Seastedt and Crossley (1984) were not designed to investigate insect taphonomy and offer only anecdotal comment.

2.3 AIMS AND SCOPE OF EXPERIMENTS

The aim of this series of experiments was to provide an overview of insect taphonomy, using a range of basic insect morphotypes and a rigorous and replicatable protocol. The laboratory conditions were strictly controlled and consistent throughout (water chemistry, bacteria, temperature and oxygen availabilty). The stages of decay and the chemical and structural breakdown of the cuticle would be qualitively and quantitively documented. Once insect decay was more clearly understood, the validity of the results were tested under more natural conditions.

Representatives of six morphologically distinct orders that are also palaeontologically important were selected (Table 2.1).

The order **Blattodea** (cockroaches) belongs to the long recognized monophyletic group, Dictyoptera, which also includes the Isoptera (termites) and Mantodea (mantids) (see Fig. 1.02). Although each order is distinctive, a number of common features (perforated tentorium, paraglossal musculature, toothed proventriculus and the female genitalia) demonstrate affinity (Gullan and Cranston 1994). The Dictyoptera is a member of the informal 'Orthopteroid Assemblage' (see Chapter 1, Fig. 1.02), which unites the sister groups Orthoptera (crickets, katydids, grasshoppers, locusts, *etc.*), highly derived Dermaptera (earwigs), and Phasmatodea (stick insects), all once considered dictyopterans (Aubertin 1946). The Blattodea therefore possess a morphology comparable to a significant component of the Insecta. Blattoids appear during the Carboniferous, where their distinctive tegmina (fore wings) comprise 80% of all insects specimens collected during this period (Carpenter and Burnham 1985; see Chapter 3).

The America cockroach (*Periplaneta americana*) was selected for study because of its size and the relative ease with which specimens can be attained and bred in captivity.

Order	Species	Common name	n
Blattodea	*Periplaneta americana*	American cockroach	30/*15*
Orthoptera	*Acheta domestica*	Common cricket	60
Coleoptera	*Coccinella 7-punctata*	7-spot ladybird	25
Coleoptera	*Tenebrio molitor*	Mealworm beetle	*3 0*
Diptera	*Calliphora vomitoria*	Blow fly	30
Lepidoptera	*Ephestia kuehniella*	Mediterranean Flour moth	30
Hymenoptera	*Formica cunicularia*	Wood ant	70

Table 2.1 Species selected for experimentation. n = number of individuals decayed. Numbers in ***italics*** refer to field-based experiments.

The order **Orthoptera** (crickets, grasshoppers and locusts) while similar in many respects to the Blattodea, has strongly developed metathoracic limbs which facilitate jumping. This development of the hind legs also occurs in some members of a number of other orders *e.g.* Coleoptera, Phasmatodea and Hymenoptera. Orthopteran tegmina first appear during the late Carboniferous where they are commonly reported (Carpenter 1992). Complete specimens are a significant component of a number of lagerstätten, notably the Cretaceous Crato Member, Santana Formation of Brazil (Martill 1988, 1990; Grimaldi 1990), and the Palaeogene lakes of North America (Chapter 6).

The common cricket (*Acheta domestica*) was selected for study because it is representative of the order as a whole (biting/chewing mouth parts; enlarged, saddle-shaped pronotum; toughened, narrow tegmina; large, fan-folded hind wings; and large hind legs modified for jumping). Colonies of crickets are readily available and maintained with relative ease.

The order **Coleoptera** (beetles) is the most diverse of insect taxa. Easily recognized by their toughened sclerotized elytra, beetles are ubiquitous. Their elytra, though rarely diagnostic, are the most common insect fossil (see Carpenter 1992; Elias 1994; Chapter 8). In many deposits, beetle elytra are the only recognizable fossils (*e.g.* Lewis and Heinken 1993).

Two species of beetle were selected for study, the 7 spot ladybird (*Coccinella 7-punctata*) and the mealworm beetle (*Tenebrio molitor*). The ladybird was selected primarily because of the colouring of the elytra. Three types of colouration are noted: pigmentation, diffraction gratings, and structural colouration (Elias 1994; McCobb 1997). The colour of the ladybird is derived soley from pigmentation (Majerus and Kearns 1989). The mealworm beetle is perhaps more representative of the order as a whole.

The order **Diptera** (true flies) is considered to be related to the orders Siphonaptera (fleas) and Mecoptera (scorpionflies) which together are formally named the Antliophora (see Chapter 1, Fig 1.02). The wing venation of the true flies is sufficiently variable morphologically to allow detailed classification, an advantage in the study of fossils, where wings are the most commonly fossilised insect component (Carpenter 1992). Dipterans are commonly preserved intact in a number of Tertiary lagerstätten, *e.g.* North American lakes (Chapter 6), and perhaps more importantly, amber (Poiner 1992).

Although the blow fly (*Calliphora vomitoria*) is a highly derived dipteran, its general morphology is nonetheless comparable to much of the order. The stout body, low wing-to-body ratio, and strong flying ability ensure that the species is particularly similar to many members of the suborder Brachycera

The order **Lepidoptera** (butterflies and moths) is sister group to the Trichoptera (caddisflies) and together they are united in the formal group Amphiesmenoptera (see Chapter 1, Fig 1.02). Ancestral amphiesmenopteran larvae are considered to have lived in damp soil amongst liverworts and mosses and ultimately radiated into water (Trichoptera) or into terrestrial phytophagy (Lepidoptera) (Gullan and Cranston 1994).

The morphology of lepidopterans is very distinctive, with a large wing to body ratio. The fossil record of Lepidoptera is the poorest of all orders (Labandeira and Sepkoski 1993).

The Mediterranean Flour Moth (*Ephestia kuehniella*) although a typical moth was selected for primarily ecomonic reasons. The thriving trade in Lepidoptera ensure that a high premium is payed for many species. Most butterfly houses stock only the more exotic (and expensive) species. The drab colouring of *Ephestia* reduces the popularity of the species and consequently the cost.

The order **Hymenoptera** (bees, ants and wasps) is amongst the most diverse of modern insects. Hymenopterans are the most socially organised insect order (Burnham 1978), and as such are commonly fossilised in significant numbers, *e.g.* the ants of the Bembridge Marls (McCobb *et al.* in review; Jarzembowski 1980; Chapter 7). Their distinctive morphology allows ready recognition.

The wood ant (*Formica cunicularia*) is amongst the most repesentative of the formicids, although its comparability to the other members of the order (wasps and bees) is more restrictive. Wasps and bees were precluded from study because of the difficulty in maintaining a viable colony for the duration of the experimental run. Ants however are particularly common in the fossil record (see Chapter 7), and therefore an investigation of their taphonomy remains of value.

2.4 DECAY EXPERIMENTS

2.4.1 Material

Live specimens were obtained from various insect houses and maintained under appropriate environmental conditions until required. Only healthy adult specimens were used for experimentation. Morbid/dead animals were discarded.

2.4.2 Method

Insects are remarkably resistant to death, *e.g.* immersion in water for periods in excess of 24 hours merely stunned the specimens, recovery occurring within hours. Experimentation on the cockroach established that an extended period of anoxia was the only reliable method of termination which leaves both internal tissue and gut bacteria undamaged. Therefore, the animals were asphyxiated in an airtight chamber utilizing an oxygen scavenging chemical (Anaerocult; BDH Merck Ltd., Poole, Dorset, U.K.) for 24 hours. The determination of the time of death is imprecise due to the extended period of dormancy preceding death. However, specimens sampled after 24 hours were dead and displayed no signs of the onset of decay. This standard time was used for all experimental runs.

Each carcass was transferred to a screw-top glass experimental vessel with 50ml of standard artificial fresh water (AFW) (see Table 2.2), inoculated with water from the Tamar Estuary, Plymouth, England. The Tamar is characterised by high rates of organic

matter degradation through aerobic processes and anaerobic sulphate-reduction. The bacteria tolerate a range of salinities (R.J. Parkes, *pers comm.*). The solution was incubated, with yeast extract added as a bacterial substrate, at room temperature for at least 48 hours prior to experimentation, following the method of Briggs and Kear (1993a).

Ingredients	Quantity
Distilled water	1l
NaCl	1g
$MgCl_2.2H_20$	0.4
$CaCl_2.2H_2O$	0.1
NH_4Cl	0.25
KH_2PO_4	0.25
KCl	0.5
Inoculum (l)	0.0011

Table 2.2 Ingredients of artificial fresh water (Lyman *et al.* 1984).

2.4.2.1 Decay protocol 1. An initial experimental run, using crickets, was conducted under anaerobic conditions by sealing the vessels in a plasticized aluminium bag with Anaerocult A, following the method of Cragg *et al.* (1992). Oxygen levels fell to approximately 8% within 2 hours and to 5-6% in 24 hours through replacement by CO_2 (~9% of starting gas volume) and H_2 (~0.5%) (Merck product information). O_2 levels were verified using an oxygen probe.

Crickets were sealed in bags in replicates of five, since sampling required termination of the experiment (n=50). Specimens were sampled fortnighly until week ten and then monthly thereafter (Table 2.3). By week 22, only superficial decay had begun. A final batch of specimens was allowed to decay for 40 weeks when only limited decay was observed. Under SEM, the cuticle appeared pristine. The constraints of time necessitated the discontinuation of anaerobic experimentation.

2.4.2.2 Decay protocol 2. The remaining experiments were conducted under rapid diffusion of oxygen, with the vessel covered only with tissue (Briggs and Kear 1993: condition 1b). However, even under aerobic conditions, oxygen is rapidly depleted around the carcass effectively producing anaerobic decay (Berner 1985; Briggs and Kear 1994). Aerobic experimentation allowed observation of the specimens without termination of the run, thereby reducing the number of specimens required. All experiments were incubated at 20± 0.5°C.

The experimental conditions and sampling of order are summarised in Table 2.3.

2.4.3 Sampling

Under anoxic conditions (decay protocol 1), Experiments were terminated to facilitate the documentation of decay. Replicates were run to allow variation to be documented.

| Species | n | oxygen | Sampling Interval (days) | | |

Under free oxygen diffusion (decay protocol 2), decay was monitored through visual inspection of *all* the specimens. Representative examples were dissected only when significant decay-induced change had occured. The interval between sample dates was determined in the light of the progress of decay. The sampling dates are recorded in Table 2.3.

Briggs and Kear (1993a) utilized dry weight change as an indication of the progress of decay. Although weight was recorded in the initial cricket experiments, the early growth of enveloping microbial films (which were impossible to remove), reduced the accuracy and hence the utility of these figures. Measurement of weight was therefore discontinued after this initial experimental run.

The state of decay was recorded and photographed. Both water colour and the presence of microbial films on the emergent carcass and vessel bottom were recorded by visual inspection. Upon removal, the specimens were freeze-dried for 12 hours.

2.5 RESULTS OF LABORATORY DECAY

2.5.1 Blattodea

2.5.1.1 Introduction. Cockroaches possess two pairs of wings: leathery fore tegmina held flat over the body, and membranous fan-shaped hind wings. The head is largely concealed beneath a large pronotum, with only the long, slender antennae extending beyond. The legs are long, spiney, and well equipped for running (Ragge 1965). Most cockroaches can fly but seem reluctant to do so and are essentially ground living creatures (McGavin 1992).

Cockroaches are a cosmopolitan group closely associated with man. Omnivorous, they find ideal homes in warehouses, kitchens and breweries where there is warmth, moisture and an abundance of food (Ragge 1965). However, these "nocturnal, malodorous, disease-carrying, refuge-seeking, peri-domestic roaches" are unrepresentative of the wider diversity of this typically tropical, often diurnal, and sometimes arboreal order (Gullan and Cranston 1994, p220).

Sub-classification of the blattoids has proved problematic (Carpenter 1992). The generally recognized classification is that of McKittrick (1964) who established five families on the basis of genital structures, nature of proventriculus, egg-laying behaviour and the structure of certain appendages. The order contains about 3500 species (Mackerras 1970).

2.5.1.2 Fossil record. Although the order is of limited diversity today, the geological record indicates that the Blattodea was one of the commonest of Palaeozoic insect orders (Carpenter 1992; Ross & Jarzebowski 1993). The vast majority of fossils (~90%) consist only of isolated wings or wing fragments. Since classification of living cockroaches is based upon body structure, not wing venation, much confusion exists.

This is compounded by the fact that where the cockroach body is fossilised, it is generally hidden beneath folded wings (Carpenter 1992). Therefore, the systematics of fossil insects has tended to emphasise slight differences in venation, the result being the erection of some 25 extinct families and 370 extinct genera from the Palaeozoic and Mesozoic, with fully half these taxa based upon single specimens (Carpenter 1992; Ross & Jarzebowski 1993). The order is currently under revision by Jörg Schneider, Bergakadamie Freiberg, Germany (see Schneider 1984 and references therein).

2.5.1.3 Morphology. The cockroach head is primitive in structure, with few specializations. The simple biting jaws are strongly toothed reflecting their omnivorous diet (Chinery 1993). The long antennae are filiform and multi-segmented. The compound eyes are well developed. The head is concealed from above by the pronotum, which also covers the meso- and metathorax, although it does not extend over the sides of the prothorax (Chinery 1993; Gullan and Cranston 1994). The leathery tegmina overlap in the mid-line protecting the membranous hind wings. The long, slender spinose legs make cockroaches elusive runners. The abutting coxae conceal the ventral thorax. The abdomen has ten segments and ends in a pair of short, many-segmented cerci.

The nymphs are worm-like upon hatching, but shed their skin upon contact with the air, emerging as tiny cockroaches. Metamorphosis is slight, with between 5 and 12 moults (Chinery 1993).

2.5.1.4 *Periplaneta americana* (Blattidae). Blattids are normally brown with darker or paler markings, many with a 'shiny' appearance. The underside of both meso- and meta-thoracic legs is spiny. Body length ranges from 24-45mm (Fig. 2.02).

Blattids are cosmopolitan, nocturnal and synanthropic, commonly infesting homes, sewers and rubbish dumps. Hiding in nooks and crannies during the day, and scavenging nocturnally, they can breed for some time before discovery. Some species emit a foul-smelling liquid which is responsible for foodstuff contamination (McGavin 1992). Active, fast runners, they fly only in very warm environments. Females produce up to fifty ootheca, each with 12-14 eggs, which are bonded to objects within concealed places (Ragge 1965).

2.5.1.5 Decay sequence (Fig. 2.02, 2.09).

0. *Freshly killed.* - Killing the insect by anoxia does not affect its appearance. The wings remain folded in the usual resting position, while the legs curl beneath the body. Upon introduction into the water-filled vessel the dorsal surface of the carcass is emergent and the legs extend below.

1. *Swelling of the abdomen.* - Expansion of the internal tissues (due to osmotic uptake) leads to stretching of the arthrodial membranes of the abdomen, particularly in the

dorsal region, producing a swollen appearance. Within fourteen days the internal organs liquefy, leaving only the crop/gut discernible. The breakdown of internal tissues produces gases which increase abdominal swelling. Upon rupture, the abdomen deflates. Volatile material may leak through the anal/genital opening to form a white cloud around the posterior. The body fat degenerates to an amorphous, white, semi-liquid which settles to the bottom of the body cavity (*i.e.* the lowest point, generally the abdomen, depending on the attitude of the insect in the vessel), stretching the arthrodial membrane still further, and creating a void above. The thoracic muscles become opaque white, and begin to disintegrate within four weeks, although fragmentary fibres may still be evident (using the binocular microscope) for some time. As the muscles break down the legs 'droop'. The antennae become flaccid and the distal segments commonly disarticulate. The resulting fragments are held in place by surface water tension.

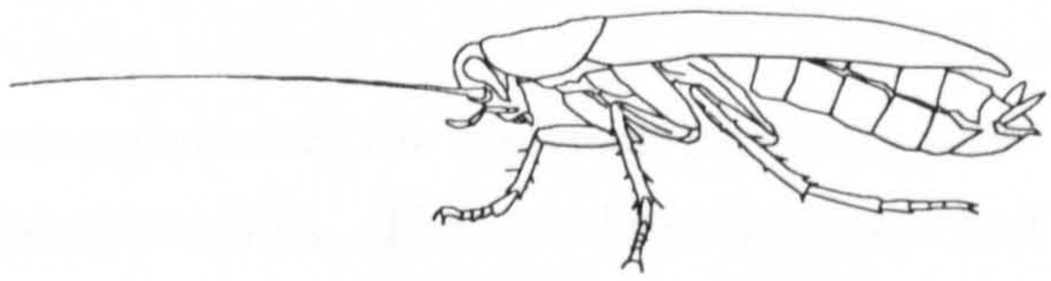
2. *Rupture of the abdomen.* - The carcass becomes flaccid but retains integrity. The abdomen is distinctly swollen. Minor rupture occurs, both between tergites (particularly junctions 3/4 and 5/6) and along the lateral margin of the abdomen, which tends to split on one side only. White internal tissue may bulge from these breaches, but its solidity prevents leakage. However, with propagation of the ruptures, and the continued breakdown of the internal tissues, the internal material leaks. The inflated crop/gut deflates upon rupture. The arthrodial membrane between the head/thorax and thorax/abdomen is stretched. The cerci begin to disarticulate, but remain trapped by surface tension. The eyes partially collapse. The mouth organs become matted to the head.

The water becomes pale yellow and cloudy. A film develops on the surface. Fungal growth is discernible on the part of the carcass exposed to the air. A thin organic precipitate covers the bottom of the vessel.

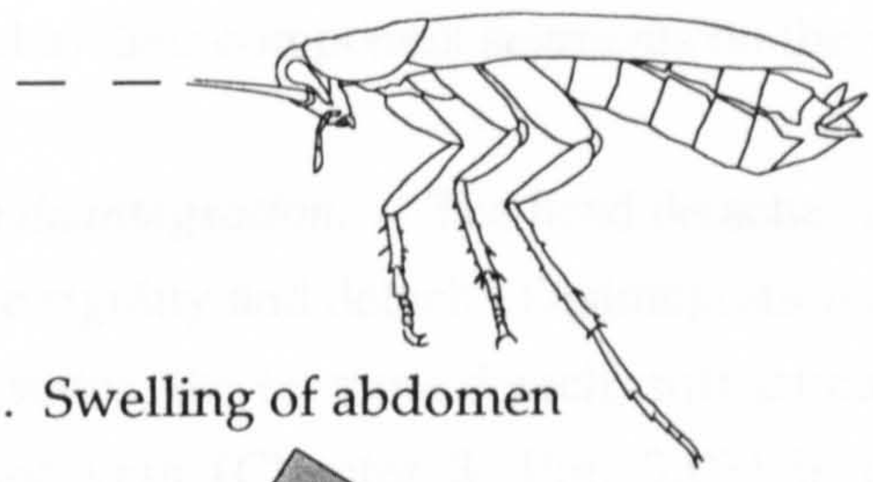
3. *Disarticulation of appendages.* - The meso- and meta-thoracic legs, followed by the pro-thoracic legs, detach at the trochanter and descend to the bottom of the vessel, unless held in position by an enveloping microbial film. Individual legs disarticulate at different rates. Disarticulation of the antennae and cerci continues. The female ovipositer becomes loosely articulated.

Abdominal ruptures continue to propagate. The tergites separate and are often only held in place by the films that envelop the posterior of the carcass. Internal tissue is absent, the cuticle an empty, water-filled sac. Upon removal from the water, the abdomen disintegrates completely.

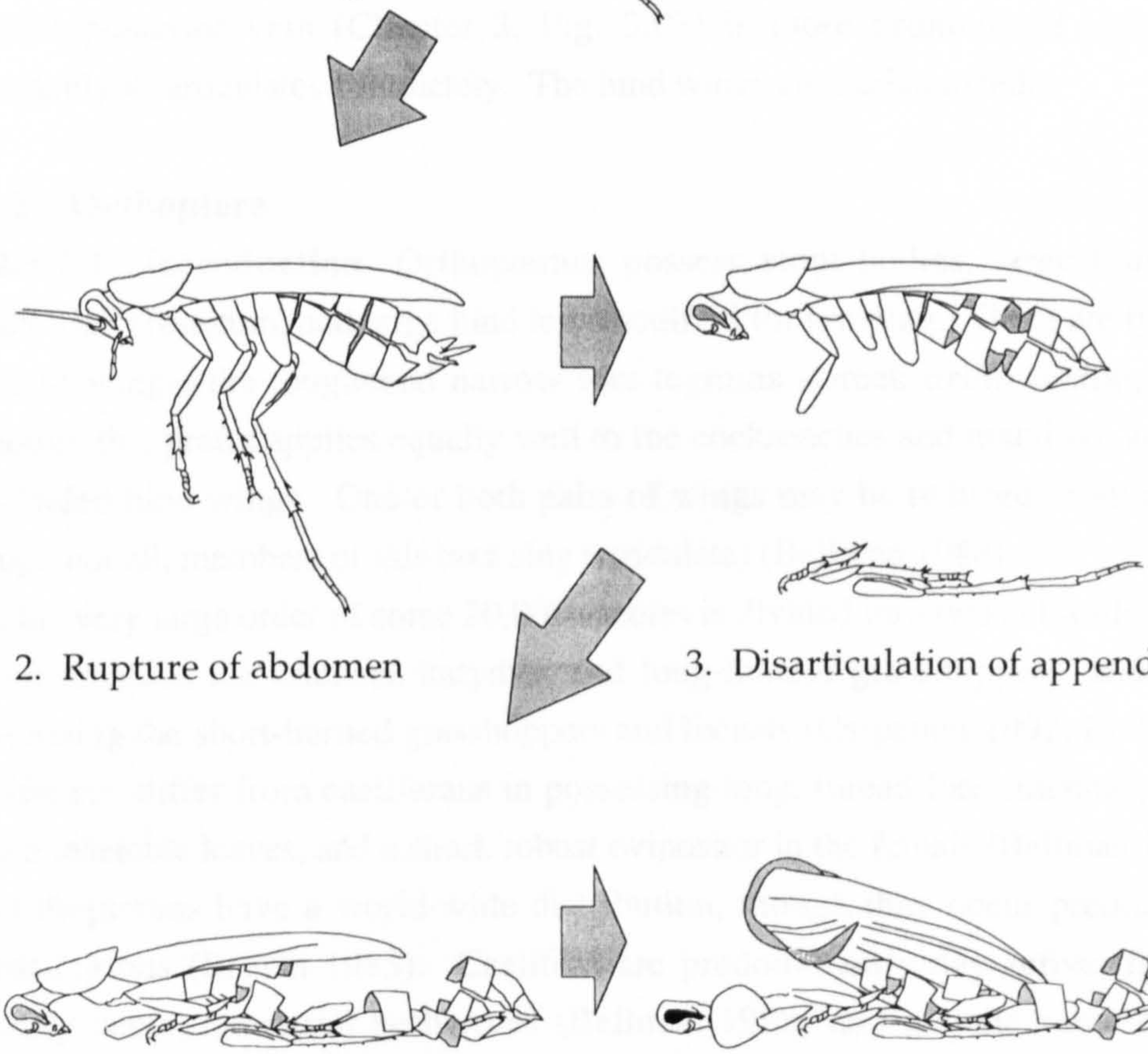
The wings remain firmly attached to the thorax. However, splitting of the forewings along the cubitus posterior vein (Chapter 3, Fig. 3.03), and partial separation of the clavus, may take place. As the arthrodial membrane stretches, so the head droops. The arthrodial membrane connecting the pro- and meta-thorax is stretched.



0. Freshly killed.

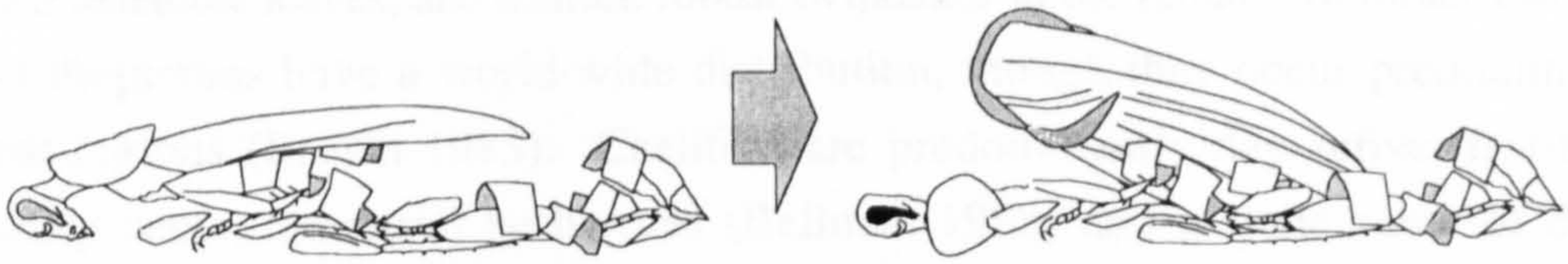


1. Swelling of abdomen



2. Rupture of abdomen

3. Disarticulation of appendages



4. Disintegration of abdomen/ buoyancy loss

5. Complete disintegration

Figure 2.02 Schematic representation of cockroach (Blattodea) decay.

Fungal colonies cover the entire emergent carcass and the surface of the water. The water becomes clearer.

4. *Disintegration of the abdomen/buoyancy loss.* - The abdomen breaks down into its component tergites. The last three segments and reproductive organs often remain superficially intact. With disintegration of the abdomen, the waterlogged carcass descends to the vessel bottom. Disarticulation of the legs progresses to the coxae. The head is only loosely articulated and readily detaches. The colour of the cuticle is faded. Disarticulation of the previously detached appendages continues, with the cerci, antennae and legs reduced to their component segments on the vessel floor.

5. *Complete disintegration.* - The head detaches from the prothorax. The meso - and meta-thorax lose rigidity and detach. Disintegration of the thorax progresses until in the most advanced states, the tegmina detach, still articulated together. Splitting along the cubitus posterior vein (Chapter 3, Fig. 3.03) is more pronounced and the clavus commonly disarticulates completely. The hind wings are skeletonized.

2.5.2 Orthoptera

2.5.2.1 Introduction. Orthopterans possess stout bodies, large blunt heads, a saddle-like pronotum, and large hind legs modified for jumping. There are typically two pairs of wings: the toughened narrow fore tegmina (Greek *ortho* = straight or rigid, although this prefix applies equally well to the cockroaches and mantids), and the large fan-folded hind wings. One or both pairs of wings may be reduced or absent. Many, though not all, members of this taxa sing (stridulate) (Bellamn 1988).

This very large order of some 20,000 species is divided into two sub-orders: Ensifera, which includes the crickets, katydids and long-horned grasshoppers; and Caeilifera, comprising the short-horned grasshoppers and locusts (Carpenter 1992; Bellman 1988). Ensiferans differ from caeliferans in possessing long, thread-like antennae, fore wings which resemble leaves, and a short, robust ovipositor in the female (Bellman 1988).

Orthopterans have a world-wide distribution, though they occur predominantly in warm regions (Brown 1983). Caelifera are predominantly day-active, fast-moving, visually acute, terrestrial herbivores (Bellman 1988) and include some of the most destructive of insects, *e.g.* migratory locusts (*Locustria migratoria*), which form immense cloud-like swarms that consume all foliage wherever they settle (Aubertin 1946). Ensifera are more often night-active, camouflaged or mimetic predators, omnivores or phytophages (Gullan and Cranston 1994).

2.5.2.2 Fossil record. Much of the orthopteran fossil record consists of isolated wings or wing fragments. Although the diagnostic morphological features of the body are

rarely preserved, wing venation is sufficiently closely correlated with body structure to enable sub-order classification in most instances (Carpenter 1992).

The Ensifera appeared during the Upper Carboniferous. Thirteen families became extinct during their history. The Caelifera originated during the Triassic. Three families have become extinct.

2.5.2.3 Morphology. The large head is usually hypognathous, with large eyes and 2-3 ocelli. The antennae vary from short, to several times body length. The large pronotum is well developed, covering both the sides and top of the prothorax in a saddle-like fashion. The tegmina overlap and bend downwards to cover the sides of the body. The hind wings are broad, generally with a greatly enlarged anal region, necessitating a pleating fold in the wings when they are at rest (Chinery 1993; Carpenter 1992).

Few orthopterans are good fliers (locusts are the notable exception) and aerial activity is confined to extensive leaps. To facilitate jumping, the metathoracic legs are considerably larger than the others, with efficient claws and powerful muscles (McGavin 1992).

The ovipositer is normally well developed and externally visible. The cerci vary in length, being long in true crickets and short in most other groups. Eggs are laid beneath the ground, in plant tissue or in crevices, utilising the female ovipositor (Aubertin 1946). Upon hatching, the young are worm-like, but they assume a near-adult morphology upon contact with the air. There are normally 4-6 growth instars before maturity.

2.5.2.4 *Acheta domestica* (Ensifera; Gryllidae). Crickets are drab shades of brown, black or green. The thin antennae are longer than the body and arise from the middle of the rounded head. Stridulatory organs occur at the base of the male tegmina, with special 'mirroring organs' to radiate the sound (Brown 1983). The posterior abdomen bears a pair of conspicuous cerci. The ovipositor is needle-like. The front wings sit flat over the back, while the hind wings appear 'rolled up'. Gryllids produce a clear, attractive song of considerable purity (McGavin 1992).

Gryllids are found in all manner of herbage in woodland, meadow and grassland. Most species are ground-dwellers, hiding under stones, logs or leaf litter, while others are subterranean or tree-dwelling. Some are found in domestic situations (McGavin 1992).

2.5.2.5 Decay sequence (Fig. 2.03, 2.09).

0. *Freshly killed.* - Anoxia does not affect the appearance of the insect. When introduced into the water-filled vessel the dorsal surface of the carcass is emergent while the legs are submerged.

1. *Swelling of abdomen.* - Expansion of the internal tissue (due to osmotic uptake) stretches the arthrodial membranes of the abdomen giving a swollen appearance. The internal organs liquefy rapidly, leaving only the crop/gut discernible. Within weeks, the body fat degenerates to an amorphous, white semi-liquid which settles to the bottom of the body cavity (generally the abdomen), leaving a void above. The thoracic muscles become opaque white, but retain their internal strength and cohesion. As the muscles break down, the legs 'droop'. The droop of the metathoracic legs is most pronounced. The distal ends of the antennae disarticulate into component segments.

2. *Rupture of abdomen.* - The abdomen is distinctly swollen and deflates upon rupture. Minor rupture may occur, not between the boundaries of the segments, but along the lateral margin between tergite and sternite, where one side alone tends to split. The internal material, which has settled to the bottom of the carcass, is too solid to leak. The inflated crop/gut deflates upon rupture. The arthrodial membrane between the abdomen and thorax is stretched. The cerci disarticulate but remain trapped by surface tension. The cuticle of the appendages becomes flaccid, the legs loosely articulated.

The water in the vessel becomes pale yellow and cloudy and a film develops on the surface. Fungal growth is discernible on the emergent carcass. A thin organic precipitate covers the bottom of the vessel.

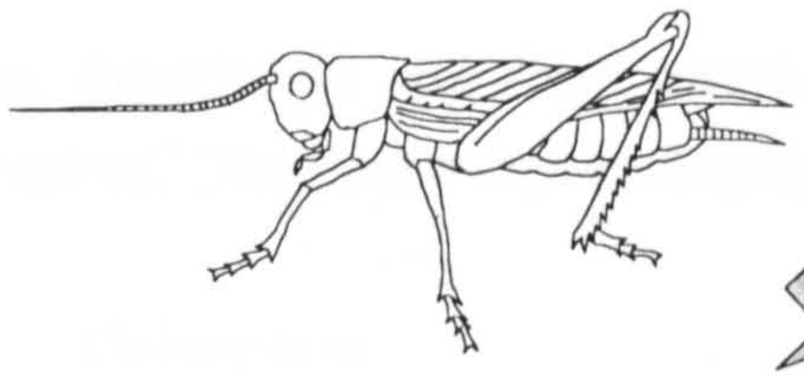
3. *Disarticulation of appendages.* - Rupture propagates along the lateral margins of the abdomen. The junctions between the posterior ventral sternites also rupture, particularly along junction 5/6. Internal material descends to the vessel bottom. The abdomen and thorax separate upon removal from the water. The metathoracic legs detach, and the other legs disarticulate upon disturbance. The other appendages (antennae, cerci, ovipositor) detach and become entrapped by the surface tension. The tegmina become 'bonded' to the carcass by tension, and cannot be separated intact.

Fungal colonies cover emergent carcass, while microbial films often hold the disarticulated limbs in place. The water clears.

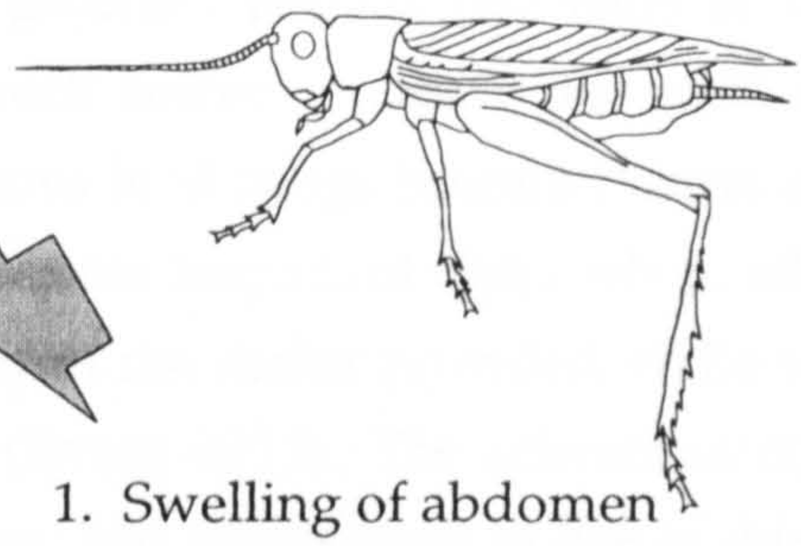
4. *Disintegration of abdomen/bacterial film control.* - A wispy, microbial film envelopes the entire carcass, hindering continued disarticulation.

The abdomen, posterior to junction 5/6, disarticulates and either descends to the vessel bottom or is held in place by the enveloping bacterial film. The membranes between the thorax/abdomen and the head/thorax are particularly stretched, the latter rupturing upon disturbance. The inter-thoracic membrane is stretched. The body is completely hollow. The appendages on the vessel bottom continue to disarticulate.

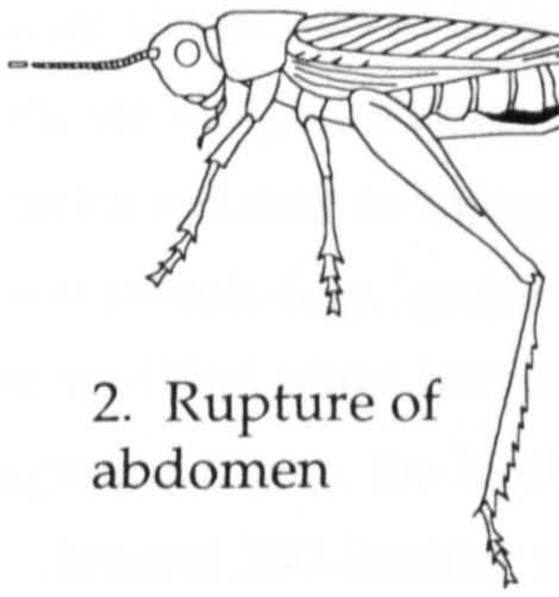
6. *Complete disintegration.* - The head detaches from the prothorax. The thorax loses rigidity and ultimately disarticulates. In the most advanced stages, the tegmina



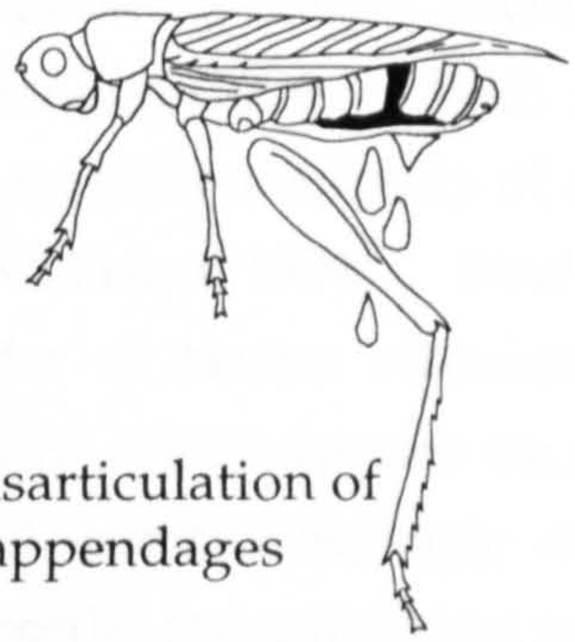
0. Freshly killed.



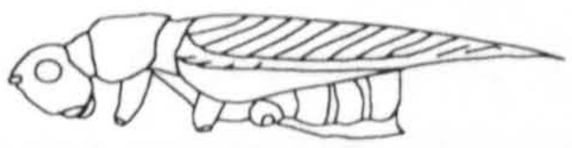
1. Swelling of abdomen

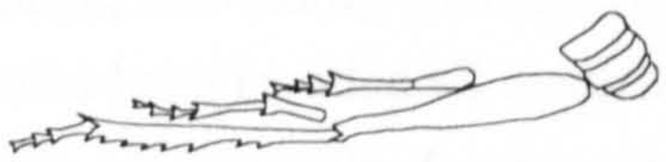


2. Rupture of abdomen



3. Disarticulation of appendages





4. Disintegration of abdomen

5. Complete disintegration

Figure 2.03 Schematic representation of cricket (Orthoptera) decay.

detach, though still articulated together. Splitting both along and between veins is pronounced. The hind wings are highly fragmented.

2.5.3 Coleoptera

2.5.3.1 Introduction. Beetles generally possess two pairs of wings. The fore wings (elytra) are hard or leathery (Greek *koleos* = sheath) and meet neatly along the dorsal midline, protecting the membranous hind wings beneath (Walsh and Dibb 1975). The success of beetles is due largely to these toughened elytra which allow them to live under stones and in litter, so making use of the shelter provided, while still retaining the delicate wings necessary for dispersal (Evans 1975). The sclerotized cuticle makes the beetles resistant to injury and desiccation, and allows them to live in drier environs than most insects (*e.g.* granaries). The elytra can also facilitate an aquatic mode of life, with the air-filled space between the elytra and body acting as an 'air tank' (Chinery 1993). In flightless forms, the hindwings are absent and the elytra, are fused at the midline.

Around 500 families and sub families of Coleoptera are recognized, ranging from the giant tropical Hercules and Goliath beetles (Scarabaeidae) at over 15cm, to the minute featherwing beetles (Ptiliidae) at <0.3mm (Maddison 1996). With some 300,000 described species, the Coleoptera is not only the most diverse family of arthropods, but also the most diverse of animals (Gullan and Cranston 1994). Four suborders are recognized: Archostemmata, a primitive suborder of beetles associated with wood; Myxophaga, a suborder of restricted diversity whose minute species are associated with drift material and interstitial voids between sand grains; Adephaga, which include a number of aquatic forms, *e.g.* predaceous diving beetles and whirligigs; and the speciose Polyphaga, containing 85% of known species (Madisson 1996).

Beetles have invaded all available habitats, including the tidally submerged coast, and exploited all possible food sources (Aubertin 1946). They are common in every vegetational micro-habitat from foliage, flowers, buds, stems, bark and roots, to galls in any living plant or dead animal tissue in all states of decomposition (Walsh and Dibb 1975). Saprophagy and fungivory are quite common, while dung and carrion are also exploited. Although parasitism is rare, carnivory is common, and beetles are widely introduced as agents of biological control (McGavin 1992). Beetles themselves may also be pests, particularly of root crops, of timber and of stored products (Aubertin 1946).

2.5.3.2 Fossil record. Most coleopteran fossils consist of isolated complete or fragmentary elytra. Crushed portions of the head and thorax are rarely found (Carpenter 1992). Unfortunately, classification is based upon features of the abdomen, head and legs, structures that are rarely preserved. Only the elytra of Archostemmata (particularly Permian forms), display venational patterning of taxonomic value (Darlington 1929, 1969). The fossils therefore provide little taxonomic or evolutionary information.

Knowledge of the extensive coleopteran fossil record is primarily the result of the work of A.G. Ponomarenko of the Russian Paleontological Institute of the Academy of Sciences (*e.g.* 1969, 1971, 1995). The Archostemmata are the first Coleoptera, and appeared in Lower Permian deposits. Although they dominated the Triassic and early Jurassic, by the end of the latter they comprised only 10% of the Coleoptera, a figure comparable to their status today (Carpenter 1992). The Adephaga appeared in the Triassic, and were dominant by the mid Jurassic. However, by the Late Jurassic, they had assumed a position secondary to the Polyphaga, which appeared in the Early Jurassic. The Polyphaga is still the dominant suborder today (Chinery 1993).

The ancestral coleopteran stock is unknown. The presence of several coleopteran families during the Permian suggests they arose early in this period, or possibly the Late Carboniferous. By the Early Cretaceous, the coleopterans were essentially modern (Carpenter 1992).

The poorly preserved Mesozoic and Tertiary beetles of Europe and North America described around the turn of the century were, with few exceptions, placed in recent genera of similar body form. However, subsequent examination of the type specimens by specialists on the recent families concerned, indicates that up to 90% of these extinct species either do not belong to the genera in which they have been placed or could equally well be assigned to several other genera (Carpenter 1992).

2.5.3.3 Morphology. The cuticle of the head of beetles is generally heavily sclerotized. Although the antennae possess no more than eleven segments, their morphology is important in classification (Carpenter 1992). Compound eyes are normally well developed, as are the biting mouthparts (Chinery 1993).

A highly visible, mobile sclerotized pronotum is always present. The metathorax is relatively large in all flying beetles and the mesothorax much reduced. The primary functional units of the body are therefore, the head, prothorax and pterothorax + abdomen, rather than the more usual, head, thorax and abdomen (Maddison 1996). When at rest, the elytra usually cover the whole abdomen, though occasionally the posterior-most segments may be exposed (*e.g.* Staphylinidae).

The legs are highly modified for digging, jumping, swimming and/or walking. The more primitive forms have five-jointed tarsi, a number that is often reduced in more specialized forms. The coxal arrangement is important in classification (Chinery 1993).

The larvae possess a well developed head, thoracic legs (except in weevils), and carry biting jaws much like the adults. Both generally eat the same food (Gullan and Cranston 1994).

2.5.3.4 *Coccinella 7-punctata* (Coccinellidae; Coccinellinae). Most ladybirds have distinctive shiny, red elytra (yellow and orange species also occur), with contrasting dark 'spots'. This bright colour warns predators of their distasteful nature

(Majerus and Kearns 1989). The head is almost completely concealed beneath the pronotum, leaving the short antennae with a terminal club, protruding beyond. The legs are short and can be drawn in tightly beneath the body (Majerus and Kearns 1989).

Holometabolous, the larvae lack a sclerotized cuticle and are often warty or spiny with dark bodies and red or white spots. They undergo four moults.

Ladybirds are found world-wide and prey on soft-bodied insects, particularly aphids. For this reason they are vitally important to man in the control of natural pests (McGavin 1992).

2.5.3.5 Decay Sequence (Fig. 2.04, 2.09).

0. *Freshly killed.* - Anoxia does not affect the appearance of the insect. When introduced into the water-filled vessel, the dorsal surface of the carcass is emergent while the legs are submerged.

1. *Internal tissue breakdown.* - The internal organs rapidly liquefy, leaving only the crop/gut discernible. The body fat/muscle degenerates to an amorphous, white semi-liquid, which may leak from the anal/genital openings. The abdomen, which is swollen due to osmotic uptake by the internal tissue, is concealed beneath the elytra. The elytra retain their rigidity but begin to separate, exposing the hind wings. The connective tissue of the pronotum and mesothorax is stretched. The antennae and mouth organs become flaccid and are often matted to the head. The eyes become lighter in colour, and partially deflated.

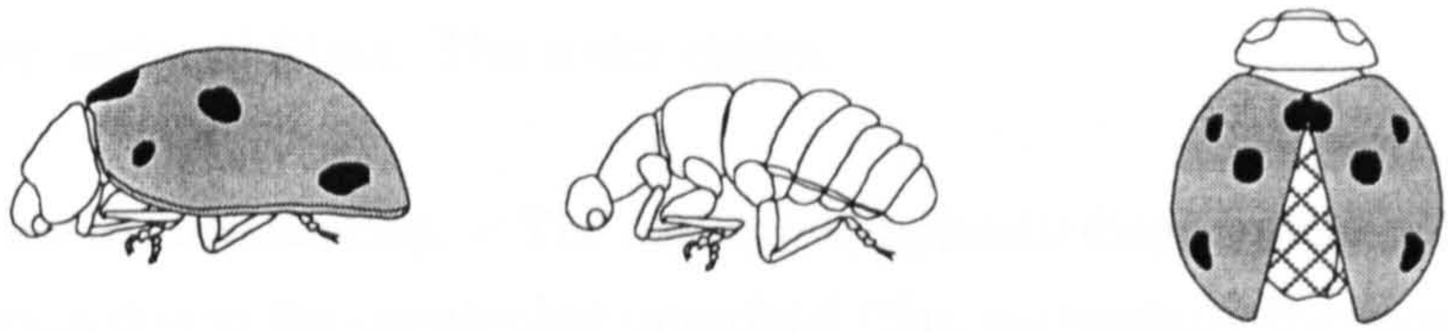
2. *Rupture of abdomen/ disarticulation.* - Rupture of the swollen abdomen occurs along its lateral margins. The internal organs cannot be distinguished. The ventral sternites remain a single unit while the dorsal tergites separate. Bacterial films envelop the submerged ventral surface of the carcass.

The distal limb segments disarticulate, generally at the trochanter, and either descend to the bottom of the vessel or remain trapped by the bacterial films. Upon removal from the vessel, the limbs disarticulate at the coxae. The connective membrane of the head/thorax and thorax/abdomen is stretched. The red colour of the elytra slowly fades. The hind wings begin to unfold beyond the elytra. Their inter-vein tissue tears, producing a partially skeletonized appearance. The posterior wing margins curl. The eyes decay, exposing the sockets, and the antennae disarticulate.

The water in the vessel becomes pale yellow and cloudy. A thin organic precipitate covers the bottom of the vessel.

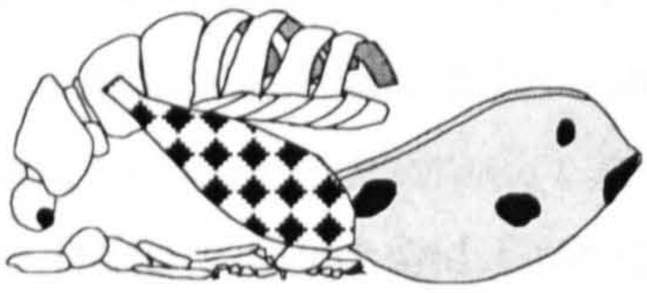
3. *Buoyancy loss/ disarticulation of elytra.* - As the abdomen continues to disarticulate, buoyancy is lost and the carcass descends to the bottom of the vessel. The elytra disarticulate. Their red colour fades to semi-transparent yellow. The black spots

0. Freshly killed



1. Swelling of abdomen/ internal tissue breakdown

2. Rupture of abdomen/ disarticulation of appendages



3. Disarticulation of elytra/ buoyancy loss

4. Complete disarticulation

Figure 2.04 Schematic representation of beetle (Coleoptera) decay.

fade too. A wispy, bacterial film envelopes the remaining carcass, save the spread hind wings.

The head is hollow but remains articulated until removed from the water. The pronotum is connected only by thin strands of tissue, and readily detaches. · The remaining thoracic segments are entirely hollow, but remain articulated to the anterior abdominal segments. The exposed hind wings continue to skeletonize, splitting irregularly along some veins. Occasionally a hind wing disarticulates. The tergites of the abdomen have now completely separated while the sternites remain a single unit (although the posterior-most segment may be lost). The abdominal segments may be held in position by bacterial films. The water clears.

4. *Complete disarticulation.* - The carcass completely disarticulates. Some parts remain in association due to the enveloping microbial film, particularly the mesothorax, generally with the proximal portions of the hind wings, the metathorax, and the abdominal tergites. The sternites remain a single unit. The hind wings split along the veins into fragments 2-5mm in dimension. Only the disarticulated, faded elytra are readily recognisable.

2.5.4 Diptera

2.5.4.1 Introduction True flies possess only two recognizable wings (Greek *di* = two), the hind wings being reduced to small club-shaped outgrowths termed halteres or balancers (Stubbs and Falk 1983). The pro- and meta-thoracic segments are reduced, while the meso-thorax is enlarged to accommodate the flight muscles. The majority of flies are strong, agile fliers.

Around 100,000 species of Diptera in some 170 families have been described, ranging from the stout bodied house-flies and bluebottles, through the slender crane-flies and mosquitoes, to a host of smaller species commonly referred to as gnats and midges (Carpenter 1992; Gullan and Cranston 1994). Two extant sub-orders are recognized: Nematocera, comprising crane flies, mosquitoes, midges, gnats and their relatives, with slender antennae and a 3-5 segmented maxillary palp; and Brachycera, heavier built flies including hover, bee, dung and blow flies, which have more solid, often shorter antennae, and a 1-2 segmented maxillary palp (Gullan and Cranston 1994). A third sub-order, the Archidiptera, is restricted to the Triassic (Rohdendorf 1961; Carpenter 1992).

Adult dipterans have colonised nearly all terrestrial habitats. All are limited to liquid food. Most feed on flower juices, but others prey on insects, scavenge decaying matter and faeces, or suck the blood of mammals (and so are vectors of disease, *e.g.* malaria, yellow fever and sleeping-sickness: Aubertin 1946).

2.5.4.2 Fossil record. The fossil record of the Diptera has contributed substantially to an understanding of their evolution (Rohdendorf 1964). The wings of

flies are often fossilized with their venation clearly preserved, allowing family or generic identification (Carpenter 1992).

The evidence presently available indicates that the Diptera were derived from ancestral mecopteroid stock, probably during the Permian, although the precise evolutionary line is not yet certain (Carpenter 1992). The earliest dipterans are those recovered from the Upper Triassic beds of Kirghiz, Russia (Rohdendorf 1961c). All belong to extinct families of Archidiptera and Nematocera. The earliest Brachycera occur in the Jurassic (Carpenter 1992). Most living families were already in existence by the end of the Mesozoic (Carpenter 1992).

2.5.4.3 Morphology. The head is relatively large, with dominant compound eyes, three ocelli, and antennae which vary greatly and are of much value in familial classification. The mesothorax is strongly developed (the pro- and meta-thorax reduced to little more than leg-bearing collars) and, together with the head and abdomen, often bears strong, serially-arranged bristles. The abdomen is composed of four to eight, or nine, visible segments.

Membranous wings are present in nearly all flies. The wing venation is simplified in more evolved species compared to the more primitive (Carpenter 1992). The hind edge of the wing, toward the body, is produced proximally into three lobes (Chinery 1993). The metathoracic halteres are the highly modified hind wings.

The legs are strongly developed in carnivorous species for grasping prey, while the feet of the common house-fly and its allies have suctorial pads enabling them to walk vertically or upside down on any surface.

The larvae (or maggots) are worm-like, with chitinous jaws. Although legless, they move by means of protuberances on the skin which are often beset with small hooks (Aubertin 1946). They are herbivorous, predaceous, parasitic, saprophagous, coprophagous, or fungivorous in all manner of habitats (McGavin 1992).

2.5.4.4. *Calliphora vomitoria* (Cyclorrhapha; Calliphoridae). Calliphorids are stout-bodied, with metallic green or blue, shiny black or dull colouration, and a few bristles. The tips of the antennae are distinctly feathered. Body length ranges from 7-12mm (Stubbs and Falk 1983).

Adults can be found on flowers, vegetation, close to animal carcasses and excrement, or indoors on fresh or cooked foodstuffs. The adults feed on pollen, nectar and rotting organic matter. Eggs are laid in carrion, dung, or on flesh. The larvae are saprophagous or flesh eaters. Many blowflies transmit enteric diseases such as dysentery.

2.5.4.5 Decay sequence (Fig. 2.05, 2.09).

0. *Freshly killed.* - Anoxia does not affect the appearance of the insect. When introduced into the water-filled vessel the dorsal surface of the carcass is emergent and the wings spread. The legs are 'folded' beneath the body.

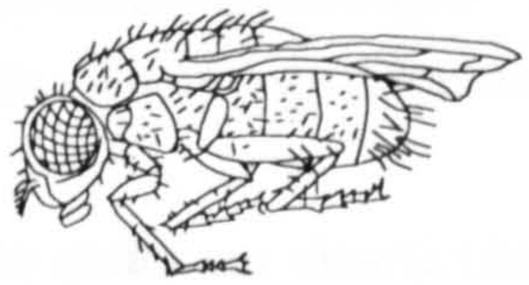
1. *Swelling of the abdomen.* - Expansion of the internal tissues (due to osmotic uptake) stretches the arthrodial membranes of the abdomen producing a swollen appearance. The internal organs liquefy rapidly, leaving only the crop/gut readily discernible. The decay gases produced further increase abdominal swelling. Volatile material may extrude through the anus/genital opening producing a 'bubble'. Within weeks, the body fat degenerates to an amorphous, brown semi-liquid. The thoracic muscles become opaque brown, and quickly disintegrate. As the muscles break down, so the legs 'droop'. The wings become flaccid.

2. *Buoyancy loss.* - The anterior carcass becomes waterlogged and breaks the surface tension, while the (still articulated) abdomen, swollen with the gases of putrefaction, remains buoyant. The penultimate segment is particularly distended. Internal material continues to extrude through the rear openings and from small tears between the third and fourth tergites. Bald patches appear on the abdomen.

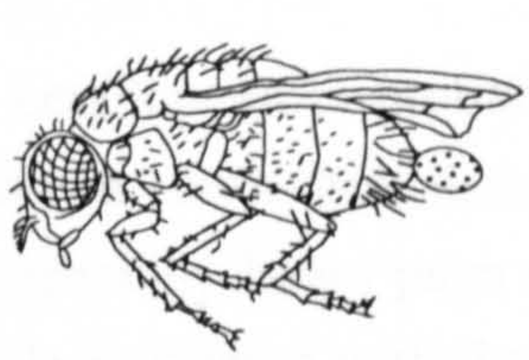
The arthrodial membrane between the head and thorax is stretched, giving the head a drooped appearance. The crop/gut is still discernible. Strands of indeterminate internal tissue remain, while a brown substance lines the ventral interior of the carcass. The wings and legs are loosely articulated. A microbial film envelops the ventral surface of the carcass smothering the limbs, disguising disarticulation of the tarsus.

3. *Rupture of the abdomen/disarticulation of appendages.* - The carcass becomes flaccid but retains integrity. The abdomen is distinctly swollen. Rupture, particularly between tergites three and four, continues. The posterior segments disarticulate upon removal from the vessel. As the abdomen disintegrates, so the carcass descends to the bottom of the vessel.

The carcass, save the spread wings, is shrouded in organic film. The arthrodial membrane between the head/thorax and thorax/abdomen is stretched, and the head droops further. The legs disarticulate at the trochanter, but remain held in position by the microbial film. The cell tissue of the wings begins to break down, producing a partially skeletonized appearance. The posterior margin of the wings crumples, and becomes ragged. The eyes are cream in colour and deflated. The water in the vessel becomes pale yellow and cloudy, while a film develops on the surface. Fungal growth is discernible on the emergent carcass. A thin organic precipitate covers the bottom of the vessel.

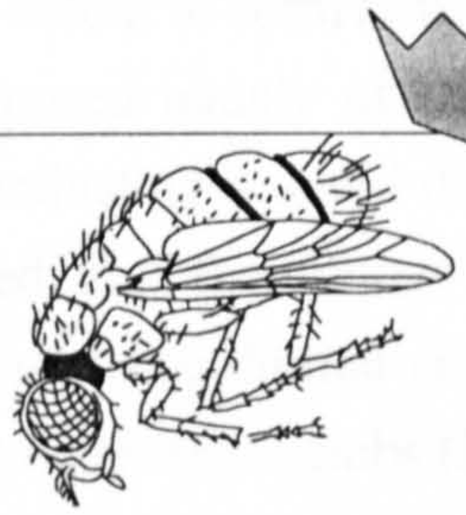


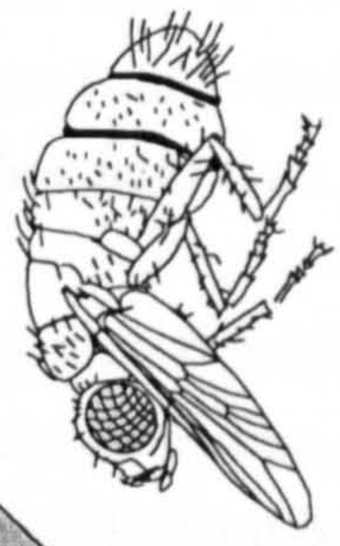
0. Freshly killed



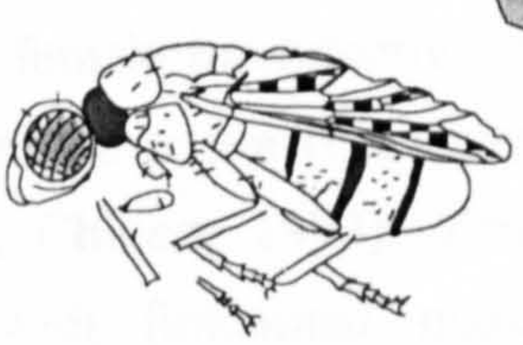
1. Swelling of abdomen

water level

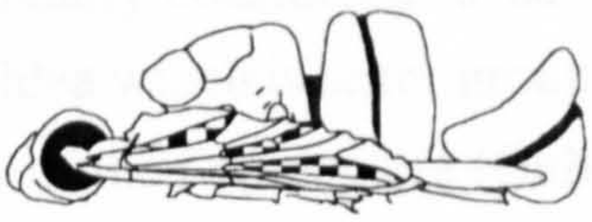




2. Buoyancy loss



3. Rupture of abdomen/
disarticulation of appendages



4. Continued disarticulation

Figure 2.05 Schematic representation of fly (Diptera) decay

4. *Continued disarticulation.* - The microbial film, which envelops the carcass, obscures the continued disarticulation of the appendages. The legs continue to dissemble; disarticulation progresses to the coxae. The wings continue to skeletonize, and ultimately disarticulate.

The posterior two segments of the abdomen disarticulate, exposing a hollow interior. The head may disarticulate.

2.5.5 Lepidoptera

2.5.5.1 Introduction. The Lepidoptera is probably the most studied group of insects, and consequently more is known about them than any other order (Ford 1957). Butterflies and moths possess two (generally large) pairs of membranous wings, which together with the body, are more or less covered with tiny scales (Greek *lepis* = scale) which vary in colour to form striking and intricate patterns (McGavin 1992). The mouth parts are composed mainly of the maxillae, which normally form a long sucking tube (proboscis) facilitating a liquid diet of nectar. Moths, which tend to be nocturnal and drably coloured, hold their wings outstretched and lack antennal clubs. Butterflies, on the other hand, tend to be diurnal and brightly coloured, and they hold their wings upright and have marked antennal clubs (McGavin 1992).

With nearly 140,000 described species, the Lepidoptera is second only in diversity to the Coleoptera. Higher classification has been controversial for some time, but the past 20 years have seen a more general agreement on a subordinal classification based mainly on the evolution of the mouthparts, the female reproductive system, and the wing venation, as well as the structure of the larvae and pupae (Carpenter 1992). Four suborders are recognized (Common 1970, 1975; Chinery 1993): Zeugloptera, the most primitive, consisting of a single family, with functional mandibles and normal maxillae; Dacnonypha and Monotrysia, with mouthparts of intermediate morphology; and Ditrysia, which includes by far the majority of lepidopterans and is characterised by complete loss of mandibles, and by development of a tube-like proboscis.

Although the butterflies are popularly considered to be distinct from moths, together they form a superfamily Papilionoidea which is sister group to the skippers (Hesperoidea) and lies deep within the phylogeny of the Lepidoptera (Gullan and Cranston 1994).

2.5.5.2 Fossil record. Fossils have contributed little to our present understanding of the evolution of Lepidoptera (Carpenter 1992). Ordinarily, little more than a single wing is preserved (except of course in amber: see Poinar 1992; Grimaldi 1995), and a number of species are known primarily from scales in coprolites (Carpenter 1992).

Evidence of Jurassic and Triassic Lepidoptera is unreliable (Carpenter 1992). The oldest unquestionable lepidopteran is an exceptionally well preserved specimen from the Lower Cretaceous of Russia (Skalski 1979a). A second Cretaceous species has been

found in slightly younger Lebanese amber (Whalley 1978). However, the Zeugloptera is the first definitive Mesozoic suborder (Carpenter 1992). The Dacnonypha and Monotrysia appear in the lower Oligocene, and the Ditrysia in the Eocene, but since the first records are of representatives of existing families, both may have originated sometime in the Mesozoic (Carpenter 1992).

The Tertiary record of the Lepidoptera is meagre; only half the recent families possess a fossil record (Labandeira and Sepkoski 1993). There are a number of possible explanations for this phenomenon: the lepidopterans inhabit environments which are not conducive to their preservation (Carpenter 1992); lepidopterans are characterised by relatively large individuals with lightly sclerotized bodies which decay readily (Labandeira and Sepkoski 1993). The latter explanation finds support in the experimental work of Martinéz-Delclòs and Martinell (1993), and in the experiments below.

Fossil lepidopteran larva, although rare have been found in several Tertiary deposits, including amber (Cockerell 1907a; Kusnezov 1941; McKay 1970).

2.5.5.3 Morphology. The head is relatively large. Much of its surface is occupied by the compound eyes, each with several thousand facets. There are two ocelli, which are generally concealed beneath the scales and hair of the head. The morphology of the antennae varies enormously, but they are usually covered with scales.

The mouth-parts generally take the form of a proboscis, which may be up to 15cm in length (Chinery 1993), and is coiled when not in use. Each half of the tube within the proboscis is hollow and composed of numerous horny rings separated by membrane. It is supported by an internal musculature which promotes coiling (Gullan and Cranston 1994). The rest of the mouth-parts are generally poorly developed, and mandibles are usually absent.

In the more primitive members of the order the prothorax is clearly obvious, but in the higher groups it is reduced to a small ring-like collar behind the head (Carpenter 1992). The mesothorax is always the largest of the thoracic segments and carries a well-developed, rounded scutellum. Overlying the base of each front wing is a large triangular sclerite termed a tegula (Chinery 1993). The metathorax is always very much smaller than the mesothorax and is tucked behind it, partially concealed. The fore legs may be reduced in certain families.

Among the more primitive Lepidoptera the two pairs of wings are of a similar size and shape, but in most other groups the front wings are noticeably longer (Carpenter 1992). The wing pairs are mechanically coupled to overlap during flight (Gullan and Cranston 1994). Each wing is clothed in overlapping scales (flattened modified macrotrichia: Gullan and Cranston 1994). The scales are hollow and generally contain colour pigments. Venation varies within the Lepidoptera, although it is not readily discernible because of the covering of scales. Fine hairs cover most of the body. The abdomen is unremarkable.

All Lepidoptera pass through four stages during development: egg, larva (caterpillar), pupa (chrysalis), and imago (Aubertin 1946).

2.5.5.4 ***Ephestia kuehniella*** **(Pyraloidea; Pyralidae)** The wings of pyralid moths are narrow, drably coloured and densely packed with scales. The front wings are triangular and the hind wings broad and rounded. The proboscis is covered with scales. The antennae are simple and thread-like. The legs are long. The larvae of *Ephestia kuehniella* (Mediterranean flour moth) feed on cereals and cereal products and can destroy large quantities of food in granaries and flour mills (Chinery 1993).

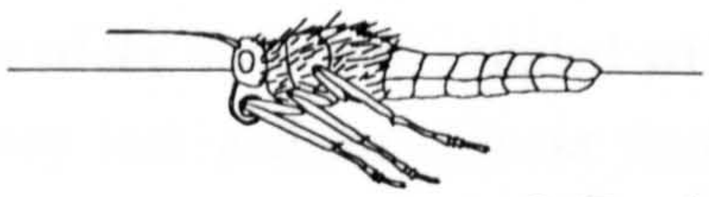
2.5.5.5 Decay sequence (Fig 2.06, 2.09).

0. *Freshly killed.* - Killing the insect by anoxia does not affect its appearance. Two death positions are noted: wings folded about the body, and wings outspread. The legs are always 'crouched' beneath the body.

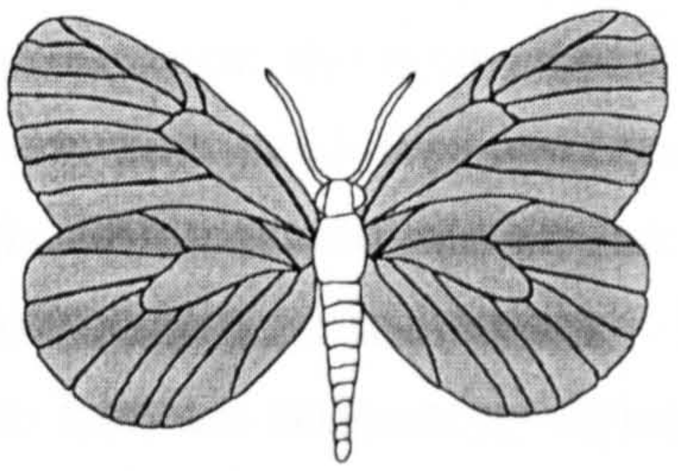
1. *Swelling of the abdomen.* - Expansion of the internal tissues (due to osmotic uptake) stretches the arthrodial membranes of the abdomen, producing a swollen appearance. The internal organs rapidly liquefy, producing gases which increase the swelling. The body fat degenerates to an amorphous brown, semi-liquid. The muscles become opaque brown, and quickly disintegrate. The amorphous internal material migrates toward the posterior of the carcass causing the abdomen to 'droop'. This material often extrudes through the anal/genital openings producing a wispy cloud. The legs begin to droop, though this is less pronounced than in other orders.

2. *Loss of wing scales* - The wings are completely covered with a double layer of scales which are readily detached (some were brushed off during the introduction of the carcass to the vessel). In carcasses where the wings shroud the body and are therefore in contact with the water, the scales begin to detach between weeks 2 and 4. Scales which cover the inter-vein cells of the wings are lost first. Where the wings are outspread, the scales of the upper are shed but remain *in situ*, giving the appearance of continuous cover. A gentle breath can dissociate them. After 10 weeks, the scale covering of the wings is generally reduced to ~50%. However, some scales may remain attached for the duration of the experiment. The fine hairs and scales which cover much of the torso are also gradually shed. This begins with the hairs of the ventral abdomen and thorax after 10-12 weeks.

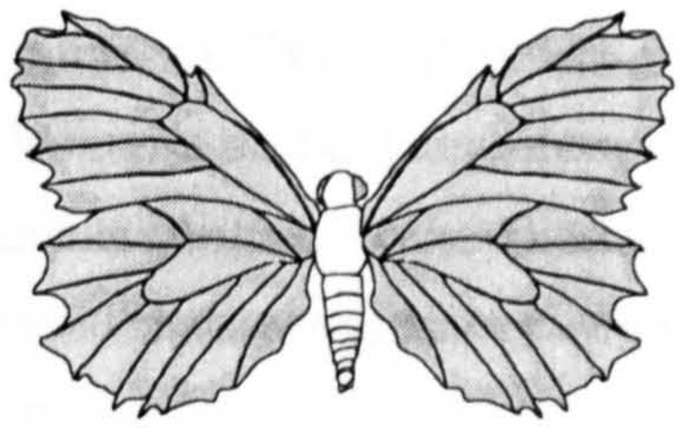
3. *Rupture of the abdomen/buoyancy loss.* - The carcass becomes flaccid but retains integrity. The abdomen is distinctly swollen and eventually ruptures along the lateral margin between tergite and sternite. Small ruptures may also be noted between the



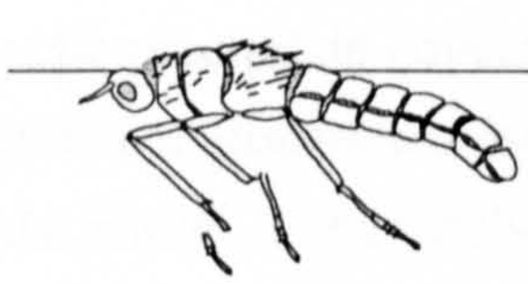
0. Freshly killed



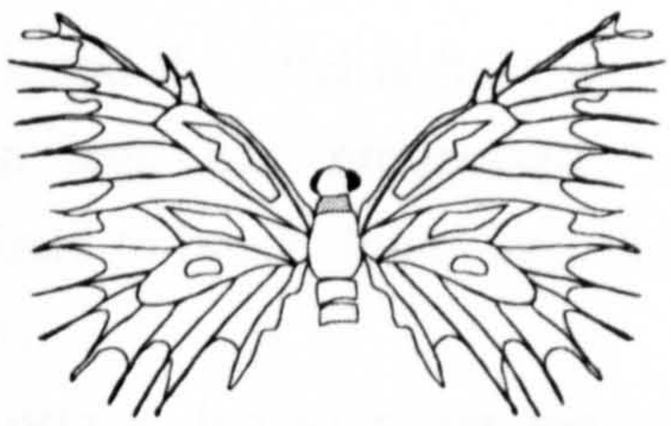
1. Swellling of abdomen

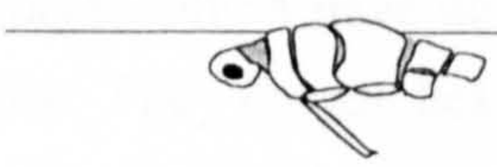


2. Loss of wings scales



3. Rupture of abdomen





4. Continued disarticulation

Figure 2.06 Schematic representation of moth (Lepidoptera) decay.

tergites. With continued rupture, internal material leaks. Upon removal of the carcass from the vessel, the posterior 2-3 segments of the abdomen disintegrate, often as a unit.

The position of the wings has a distinct influence on the next step. In specimens where the wings are shrouded about the carcass, continued disintegration and water-logging of the abdomen, coupled with the weight of the enveloping organic film, causes buoyancy loss and the carcass descends to the bottom of the vessel. However, in specimens with outspread wings, there is no loss of buoyancy; disintegration and ultimately disarticulation of the carcass continue on the surface, with the detached fragments frequently held in position by the organic film.

The cells of the wings are progressively exposed, producing a partially skeletonized appearance. The margin of the wings begins to crumple, and become ragged, with the veins appearing like spokes.

The carcass and the outspread wings are shrouded in microbial film. The arthrodial membrane between the head/thorax and thorax/abdomen is stretched, and the head droops. The eyes are deflated. The antennae begin to disarticulate but remain held in position by water tension. The proboscis unfurls, and disarticulates upon removal of the carcass from the vessel. The fine hairs of the carcass continue to be shed. The legs start to disarticulate, beginning with the distal segments and progressing proximally. The segments remain held in position by organic films.

The water in the vessel is cloudy, while a film develops on the surface of the water and upon the outstretched wings. Fungal growth is discernible on the emergent carcass. A thin organic precipitate covers the bottom of the vessel.

4. *Continued disarticulation.* - Carcasses that remain on the surface continue to disarticulate *in situ*. The loosely articulated tergites and sternites of the abdomen detach, generally leaving only the first two tergites articulated to the thorax. The individual components may descend to the bottom of the vessel but are more commonly held *in situ* by the enshrouding organic film. The loosely articulated head detaches upon removal from the vessel. The eyes are entirely deflated, and the head is hollow. The antennae completely disarticulate. Detachment of the legs has progressed to the coxae. Appendages which have already detached continue to break down into their component segments. They too are held in position by films.

The wings which have remained on the surface due to water tension are all but denuded of scales. Small tears appear and propagate in the inter-vein tissue, leaving behind only the supporting veins. The wings have a crumpled appearance. Fungi colonize the emergent surfaces. The wings remain firmly articulated to the thorax.

If the weight of carcass plus encapsulating organic film becomes sufficient, the water tension can be broken, and the remains of the carcass descend to the bottom of the vessel, where disintegration continues. However, specimens composed only of wings and thorax may remain floating even after six months.

Carcasses which have already descended to the bottom of the vessel follow a similar disarticulation pathway, although the enshrouding films frequently obscure detail.

2.5.6 Hymenoptera

2.5.6.1 Introduction. The Hymenoptera is the third largest insect order, with over 100,000 known species (Chinery 1993), and possibly twice that number awaiting discovery (McGavin 1992). The order contains not only the ants, wasps and bees, but also saw-flies, wood- and ichneumonid-wasps, and a host of species which are parasitic or gall-forming at some stage in their history (Aubertin 1946). Most hymenopterans possess two pairs of membranous wings (Greek *hymen* = membrane) with a much reduced venation, comprising comparatively few, large cells (McGavin 1992).

In behavioural terms, the hymenopterans are the most advanced insects, with lifestyles ranging from solitary to social, herbivorous to carnivorous or parasitic (McGavin 1992). Indeed, besides the termites, they encompass all the eusocial insects (Burnham 1978). Eusociality in insects involves a division of labour within the colonies, with a caste system comprising a restricted group of one or several queens, aided by workers (sterile individuals that assist the reproducers) and, in the case of ants (and termites), an additional defensive soldier group (Gullan and Cranston 1994). The success of the colony is dependent upon the co-operation of its individual members.

The order Hymenoptera is split into two sub-orders: Symphyta (sawflies, wood-wasps and other primitive forms) which lack a 'waist' between thorax and abdomen, and Apocrita (bees, wasps, ants, ichneumon flies, and other specialised forms), which possess such a 'waist' (see below) (Gullan and Cranston 1994). The Apocrita can be further sub-divided into the Parasitica (which are nearly all parasites and possess an ovipositor adapted for piercing host tissue, *e.g.* ichneumons and chalcids) and the monophyletic Aculeata (where the ovipositor is usually modified as a sting, *e.g.* bees and wasps). There is, however, no hard and fast division between these groups and overlap is noted, *e.g.* some bethyloideans are parasitic, though structurally closer to the Aculeata (Chinery 1993).

2.5.6.2 Fossil Record. The earliest appearance of the order is in the Triassic of Australia (Riek 1955) and Central Asia (Rasnitsyn 1964). All the species belong to the extant family Xyelidae (suborder Symphyta), which was considerably more diverse then than now.

A major advance in the evolution of the Hymenoptera occurred with the development of the 'waist' which presumably had the selective advantage of increasing the flexibility of the abdomen, important for both oviposition and defense (Burnham 1978). The suborder Apocrita, which possesses this adaptation, is first known from the Upper Jurassic deposits of Central Asia (Rasnitsyn 1975, 1977). These Jurassic specimens

have been assigned to the more primitive division, Parasitica. The oldest known aculeate hymenopteran was discovered in the Lower Cretaceous deposits of Siberia (Sharov 1962). Morphological and geological evidence suggests that the Apocrita were derived from symphytan ancestors related to the family Sircidae early in the Jurassic (Carpenter 1992).

The diversity of the Triassic Hymenoptera suggests that the order arose in the early Trias, or late Permian (Carpenter 1992). Rasnitsyn (1980b) proposed that the ancestral line was within the extinct Miomoptera, known from the upper Carboniferous and Permian. The resolution of this question awaits further fossil evidence.

The earliest known fossil ants occur in the Cretaceous amber of New Jersey (Wilson *et al.* 1967). These ants are primitive and possess both wasp-like mandibles and an ant-like petiole. The discovery of an early Tertiary ant colony with larvae and workers provides further evidence of the antiquity of social behaviour (Wilson and Taylor 1964).

2.5.6.3 Morphology. The heavily sclerotised head is attached to the thorax by a slender 'neck' and swivels freely. The compound eyes are generally large, and there are usually three ocelli present. The antennae are highly variable though generally longer in the female (Chinery 1993). The mouth-parts are adapted for chewing and biting, although some groups ingest liquids, *e.g.* bees possess a 'tongue' through which nectar is sucked (McGavin 1992).

The thorax is composed of three segments. However, in the Apocrita, the first abdominal segment is fused with the thorax and is known as the propodeum. The characteristic 'waist' is not strictly therefore between the thorax and the abdomen but between the first and second abdominal segments: Chinery 1993. The pronotum is often small. The mesonotum is divided into a scutum and a scutellum, and usually conceals the smaller metanotum.

There are usually two pairs of wings, although several groups, notably the ants, produce wingless individuals (Chinery 1993). The hind wings are considerably smaller than the fore wings and the two pairs are linked by a number of minute hooks (hamuli) on the front edge of the hind wing (Gullan and Cranston 1994). The venation has deviated so much from the basic pattern that it is difficult to decide which vein is which, and there is no widely accepted nomenclature (Chinery 1993). The primitive sawflies have the most complete venation (Gullan and Cranston 1994). The legs are basically cursorial, but may be adapted for digging or nest building, as in some wasps (Carpenter 1992).

The abdomen, except the first segment (discussed above), is termed the gaster, and is greatly constricted at the front to form the waist. The length of the constricted waist (or petiole) varies between groups and can involve two segments in some ants (Chinery 1993). Sawflies lack any such constriction.

Females usually possess a well-developed ovipositor. The saw flies are named after their saw-like ovipositor which they use for cutting plant tissue. Among the other Hymenoptera, the ovipositor is either used for drilling into plant/animal tissue, or is modified as a sting, and is no longer used for laying eggs. Hence, only female insects can sting.

Hymenopterous larvae are of two distinct types. Sawfly larvae are like caterpillars, with well developed heads and thoracic legs, and often fleshy abdominal legs as well. Apocritan larvae are legless and their heads are much reduced. This is because the larvae are invariably surrounded by food and do not have to search for it.

2.5.6.4 ***Formica cunicularia*** **(Formicidae; Formicinae; Formicini).** This ant is small (<7mm) and dark brown/black in colour. The species is commonly found on heathland where it is found beneath stones and in dry turf banks, where it hunts insects and other prey (Bolton and Collingwood 1975). It can also 'tend' plant-lice on vegetation (Donisthorpe 1927). The flight period of this species is July, and new colonies are founded by single queens. In mature colonies, only one queen is normally present in each nest.

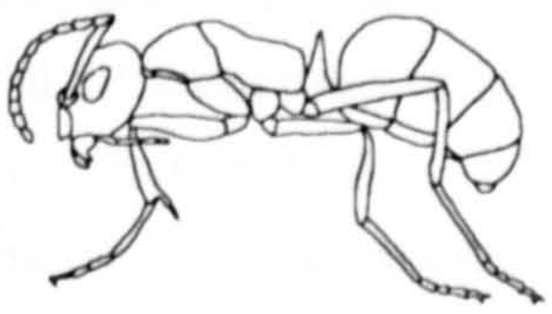
2.5.6.5 Decay sequence (Fig. 2.07, 2.09).

0. *Freshly killed.* - Killing the insect by anoxia does not affect its appearance. The ant may be bent at the petiole, producing a folded appearance. The legs are 'crouched' beneath the body.

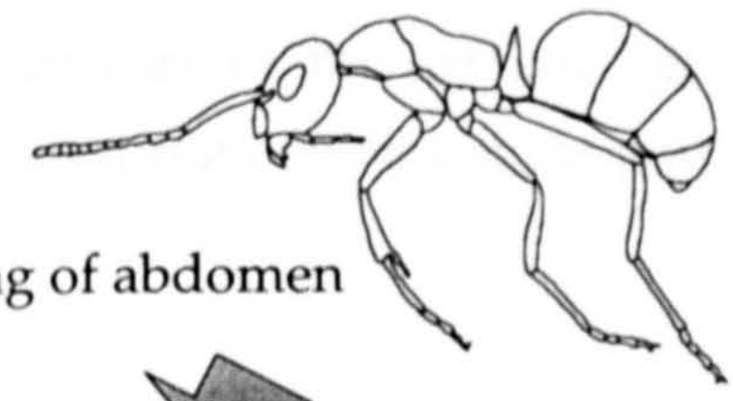
1. *Swelling of the abdomen.* - Expansion of the internal tissues (due to osmotic uptake) causes a swelling of the abdomen which exposes the arthrodial membrane between the tergites. The internal organs liquefy, leaving only the crop/gut discernible. The body fat and thoracic muscles degenerate to an amorphous, cream semi-liquid. The abdomen is commonly the first part of the carcass to break the miniscus. The legs remain curled beneath the carcass and slowly extend with continued decay of the musculature. The water remains clear.

2. *Buckling about the petiole.* - The carcass remains intact but folds about the petiole, producing a jack-knifed appearance. The carcass is flaccid but retains integrity. The abdomen is distinctly swollen, with arthrodial membrane exposed between the separating segments and along the lateral margins. Liquification of the soft tissue leads to a drooping of the appendages, including the antennae. Internal material may leak from the anal and genital openings.

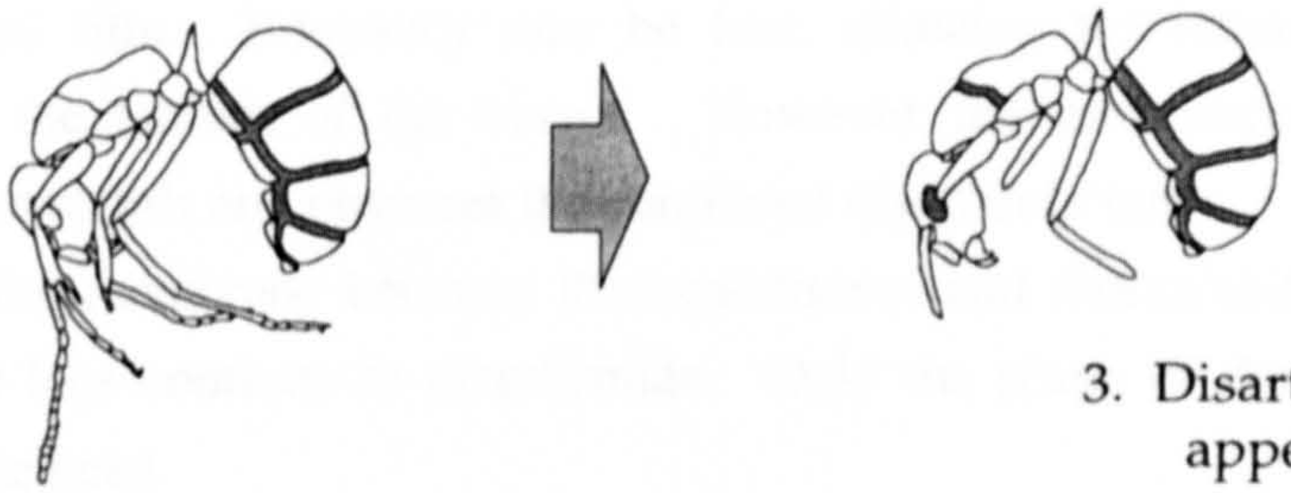
Green microbial films enshrouds the carcass, obscuring continued disarticulation. The water in the vessel becomes pale yellow and cloudy. An organic precipitate covers the vessel bottom.



0. Freshly killed

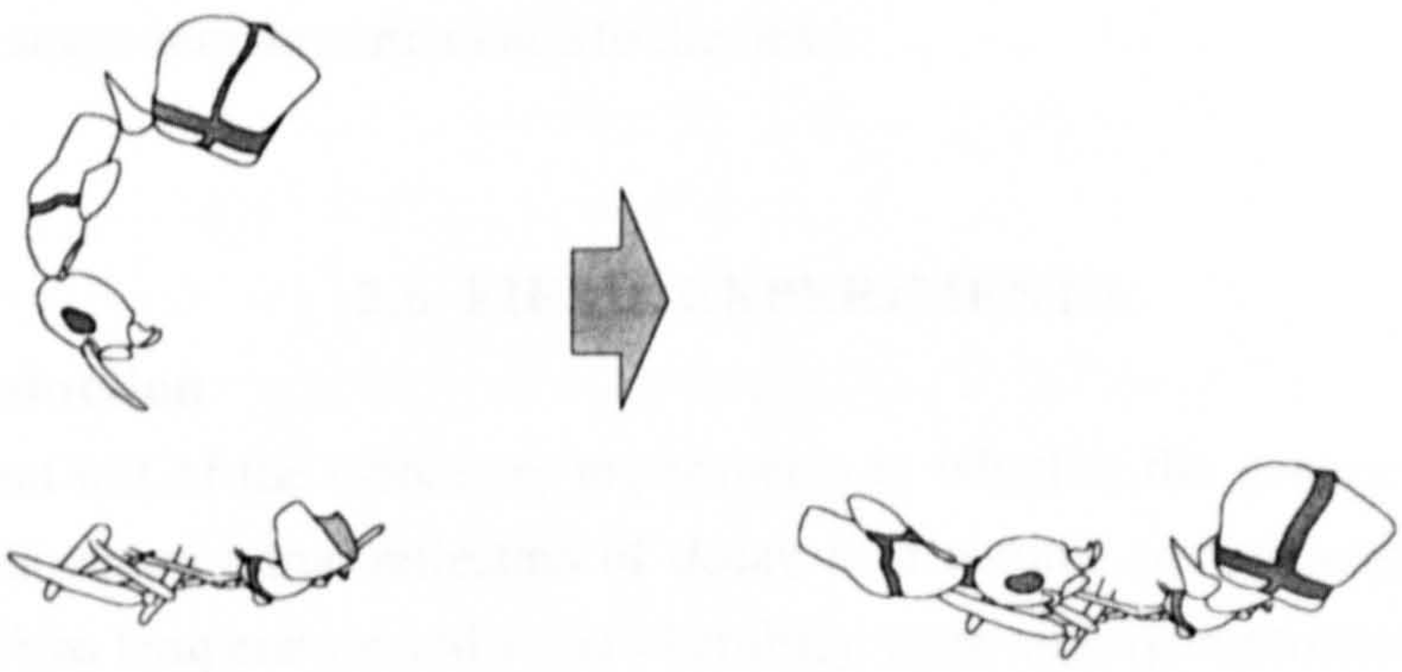


1. Swelling of abdomen



2. Buckling about petiole

3. Disarticulation of appendages



4. Disintegration of abdomen

5. Continued disarticulation

Figure 2.07 Schematic representation of ant (Hymenoptera) decay.

3. *Disarticulation of appendages.* - The limbs and antennae disarticulate at their distal ends. The limbs disarticulate at different rates and in a random fashion. The appendages remain held in position by the microbial film. The abdomen continues to swell and ruptures are apparent, particularly between segments three/four and five/six. The two posteriormost segments may separate leading to buoyancy loss. The thorax also shows distinct evidence of swelling.

The internal tissue retains no recognisable structure. This amorphous material sinks toward the lowermost part of the carcass, generally the abdomen, augmenting the swelling. Upon removal from the vessel the posterior segments of the flaccid abdomen disarticulate.

4. *Disintegration of abdomen/buoyancy loss.* - The abdomen posterior to junction 4/5 disarticulates and either descends to the vessel bottom or is held in place by the enveloping algal film. Buoyancy may be lost, allowing the remains of the carcass descending to the bottom of the vessel. However the enshrouding microbial film frequently prevents this and obscures the continued disarticulation.

The arthrodial membrane between the head/thorax and thorax/abdomen is distinctly stretched. The legs continue to disarticulate. Only the scape of the antennae remains articulated to the head.

5. *Continued disarticulation.* - The remaining part of the abdomen disarticulates from the petiole. The thorax separates from the head and disarticulates into its constituent components. The head remains clearly recognisable. The eyes show no evidence of collapse. The scape remains articulated to the head.

2.6 FIELD EXPERIMENTS

2.6.1 Introduction

An important test of the laboratory experiments is whether the general sequences of decay noted above are a true reflection of decay in a natural environment. Laboratory conditions such as temperature and water chemistry were strictly controlled. Macrobiota was absent. However, in the field, both temperature and water chemistry fluctuate with season and time of day. Standing water supports a wide variety of scavengers ranging from fish and amphibia through nematodes, actinomycetes and protozoa to bacteria, all of which are known to feed on insects from time to time. Therefore a series of experiments was initiated to assess the veracity of the laboratory findings.

To this end, experiments were conducted in a long-standing pond during the autumn and winter months of 1996/97. A single species of orders Coleoptera and Blattodea was selected as representative of sclerotized and non-sclerotized insecta as a whole.

2.6.2 Materials

Specimens of the mealworm beetle *Tenebrio molitor*, and *Periplaneta americana* (Blattodea: see above), were selected as average representatives of their respective orders (Table 2.3). Lack of availibility necessitated the selection of tenebrionids over coccinellids.

2.6.2.1 Tenebrio molitor (Coleoptera; Polyphaga; Tenebrionidae). Mealworm beetles are matt black and of medium size (~15mm). Body shapes range from small, parallel sided and blunt ended to large and broadly oval. The elytra have distinct longitudinal striations and the hind wings are often reduced (Fig 2.8).

The larvae are elongate and cylindrical, usually with tough bodies and short legs (Chinery 1993).

Tenebrionids are cosmopolitan. Many are adapted to life in very dry conditions, such as in deserts and grainstores. The beetles are scavengers, eating a range of organic materials, such as decaying vegetation, fungi, seeds, plant roots, the larvae of other insects and many stored products (McGavin 1992).

2.6.2.2 Periplaneta americana. For a description of the American cockroach, see Section 2.4.1.4.

2.6.3 Method

Live, healthy specimens were placed in separate glass jars, which were then covered with muslin (mesh size <4mm) and secured with water-resistant sticky tape (for cockroaches) or elastic bands (for beetles). A small amount of organic pond material was introduced to the jars to ensure rapid inoculation. The jars were then slowly lowered to the bottom of the pond. Insect activity was supressed by the low temperatures, ensuring that the insects made no attempt to escape. As the jars fill with water, so the insects float. The muslin cover prevents the insects from escaping or floating free.

The pond is located in the grounds of Goldney Hall, part of the University of Bristol. It is constructed of cement and measures ~6 x 30m, with a depth of 0.9m. The long-standing nature of the pond has ensured a thick bottom cover of organic material to a depth of 10cm, and a flourishing freshwater ecosystem.

2.6.4 Sampling

The sampling intervals are iterated in Table 2.3. Selection of sampling dates was based upon examination of the carcasses at each interval combined with the evidence from the laboratory experiments. Six beetles and three cockroaches were removed for study at each interval, thus terminating the experiment. Decay state was documented, and the

elytra and pronota were removed for py-GC/MS and colorimetric analysis (see Appendix A1). The following decay sequences should be read in conjunction with Figures 2.04 and 2.02.

2.6.5 Decay sequence

2.6.5.1 Beetle

1. *Swelling of abdomen/internal tissue breakdown.* - The specimens are intact and retain integrity. The connective tissue between the segments of the body is stretched. Expansion of the internal tissue (due to osmotic uptake) stretches the abdomen, exposing the arthrodial membrane and creating a swollen appearance. The elytra retain their rigidity but begin to separate, exposing the hindwings beneath. The antennae and organs of the mouth become matted to the head.

The internal organs are liquefied, leaving only the crop/gut discernible. The body fat/muscle has degenerated to an amorphous, brown semi-liquid, which may leak from the anal/genital opening.

2. *Rupture of abdomen/ buoyancy loss.* - Separation of the swollen abdomen occurs along its lateral margin between tergite and sternite, facilitating leakage of internal material. This abdominal rupture and loss of internal material causes the carcass to lose buoyancy and descend to the bottom of the vessel. The sternites remain a single unit while the dorsal tergites begin to separate. Stretching of the connective arthrodial membrane, particularly between the thorax and abdomen, gives the carcass an overall 'drooped' appearance. The hind wings begin to unfold beyond the elytra. The inter-vein tissue begins to tear, producing a partially skeletonized appearance. The elytra remain articulated. The eyes decay, exposing the sockets, and the antennae disarticulate.

Fine white nematodes (~3mm) are intimately associated with the internal soft tissue. Waterfleas are also observed.

3. *Disarticulation of elytra.* - The head and prothorax detach from the rest of the carcass as a loosely articulated unit, but their constituent elements separate upon agitation. The remaining thoracic segments are entirely hollow, but remain articulated to the anterior portion of the abdomen. The metathoracic legs detach at the coxae, while the distal segments of the other legs disarticulate. The elytra detach, exposing the hind wings, which continue to skeletonize, splitting irregularly along some veins. The tergites of the abdomen have now completely separated while the sternites remain a single unit.

4. *Complete disarticulation.* - The carcass completely disarticulates. Some parts remain in association, *e.g.* leg segments. The hind wings are completely skeletonised. Only the elytra, head and pronotum are readily recognizable.

2.6.5.2 Cockroach

1. *Swelling of the abdomen.* - Expansion of the internal tissue (due to osmotic uptake) stretches the arthrodial membrane of the abdomen and produces a swollen appearance. Minor ruptures may appear between 4/5th sternites. The legs begin to 'droop'. The antennae and mouth organs are flaccid.

The internal organs liquefy, and body fat degenerates to an amorphous, white, semi-liquid. Only the crop/gut are discernible. Volatile material may leak through the anal/genital openings.

2. *Rupture of the abdomen/buoyancy loss.* - The carcass becomes flaccid. The last three segments of the swollen abdomen disarticulate as a single unit, resulting in a loss of buoyancy. Rupture between segments and along the lateral margins of the abdomen allows internal material to leak. Material also leaks from the anal/genital openings. The connective tissue between the various body segments is stretched, giving the body an overall drooped appearance. The tegmina begin to separate, exposing the crumpled hindwings. The antennae and cerci disarticulate.

3. *Disarticulation of appendages.* - The meso- and meta-thoracic legs, followed by the pro-thoracic legs, detach at the trochanter. Thereafter they continue to disarticulate at different rates. The wings remain firmly attached to the thorax. The elytra split along the cubitus posterior vein (Chapter 3, Fig. 3.03), leaving the clavus only loosely attached.

Abdominal ruptures continue to propagate, particularly along the ventral surface, leaving the segments only loosely articulated. Internal material continues to leak.

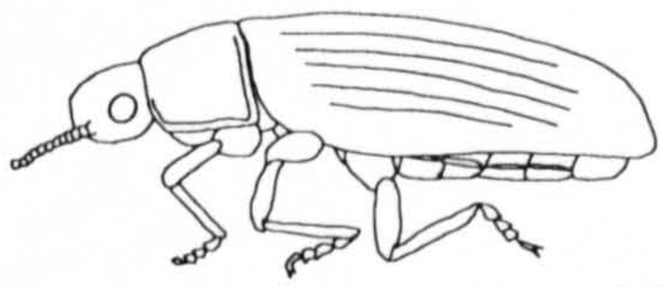
The connective arthrodial membrane is particularly stretched That of the head/thorax and thorax/abdomen split upon removal from the vessel. The arthrodial membrane connecting the prothorax to the rest of the thorax is also stretched. The antennae and cerci have entirely disarticulated.

4. *Complete disintegration.* - The head separates from the prothorax. The meso- and meta-thorax lose rigidity and detach. Disintegration of the thorax progresses until, in the most advanced state, the tegmina detach still articulated together. The clavus has detached and is often absent. The fore and hind wings have a ragged appearance. The abdomen breaks down into its component segments. Disarticulation of the legs progresses to the coxae.

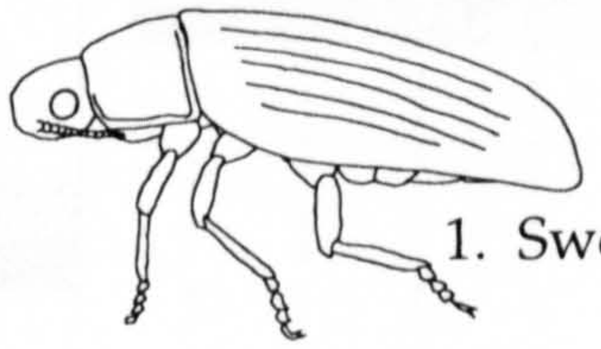
2.7 CUTICLE BREAKDOWN

2.7.1 Introduction

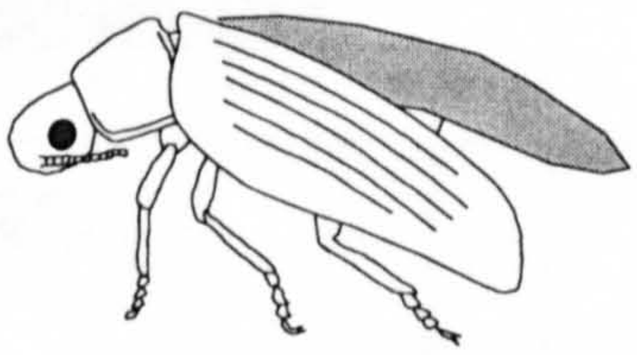
Insect cuticles, like those of other arthropods, are composed predominantly of protein and chitin biopolymers (Schaefer *et al.* 1987; Chapter 1, section 1.4). These molecules



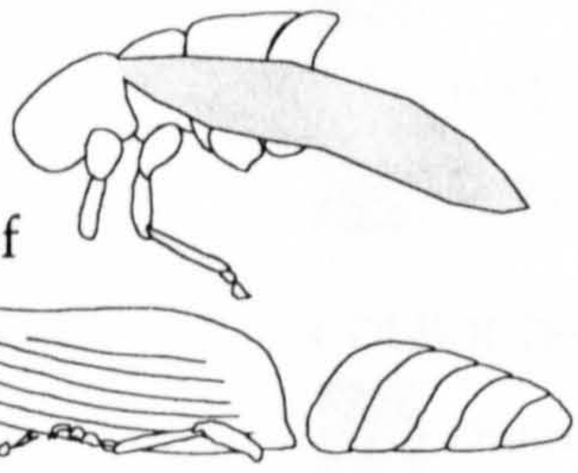
0. Freshly killed



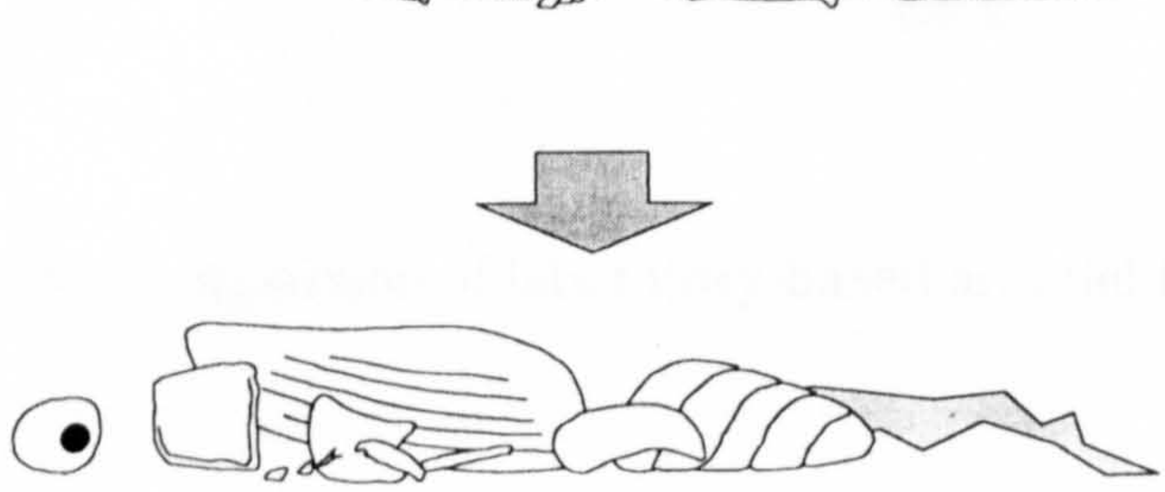
1. Swelling of abdomen



2. Rupture of abdomen/ buoyancy loss



3. Disarticulation of elytra



4. Complete disarticulation

Figure 2.08 Schematic representation of beetle (Coleoptera) decay in a natural environment.

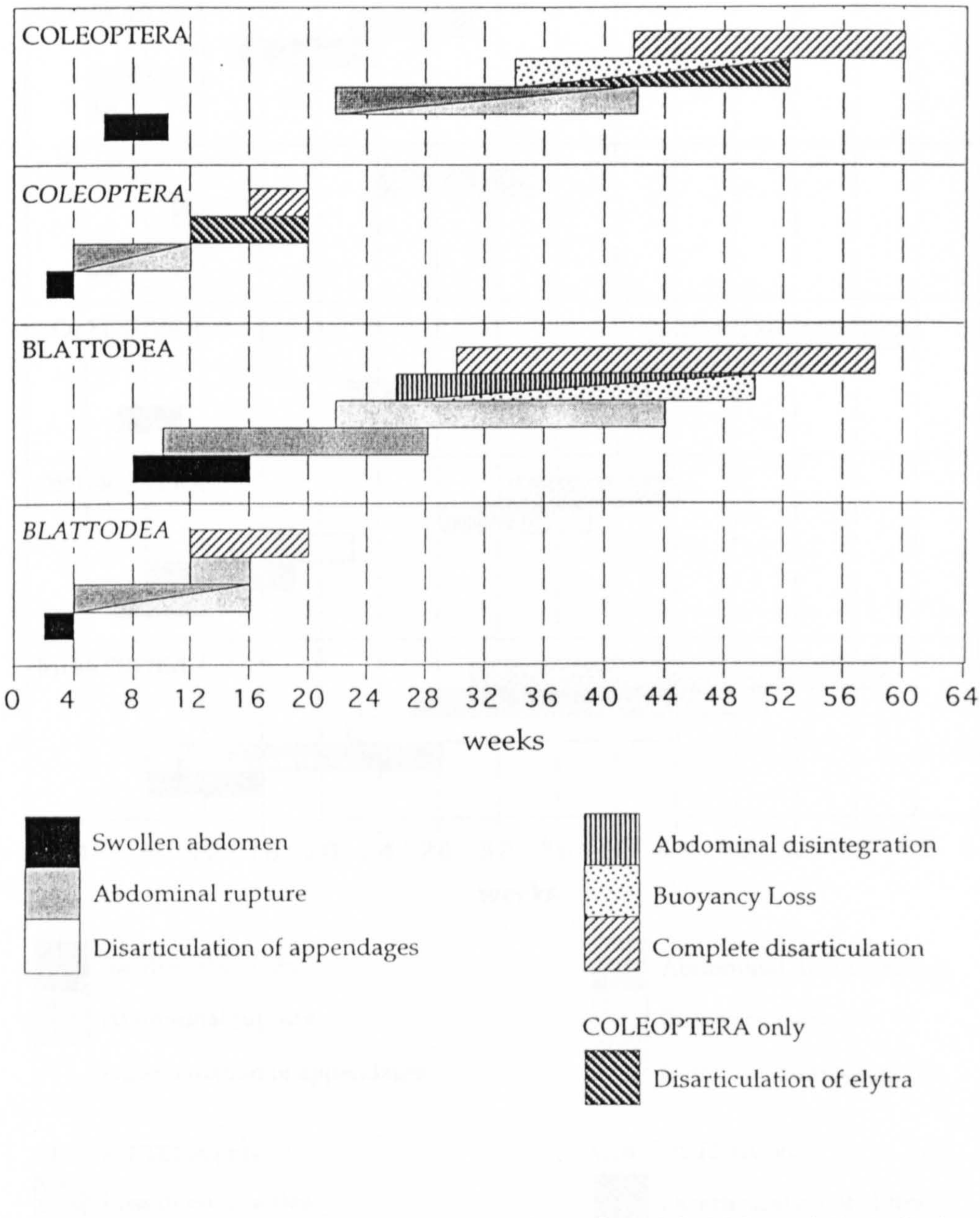


Figure 2.10 Comparison of laboratory-based and field-based (*in italics*) decay.

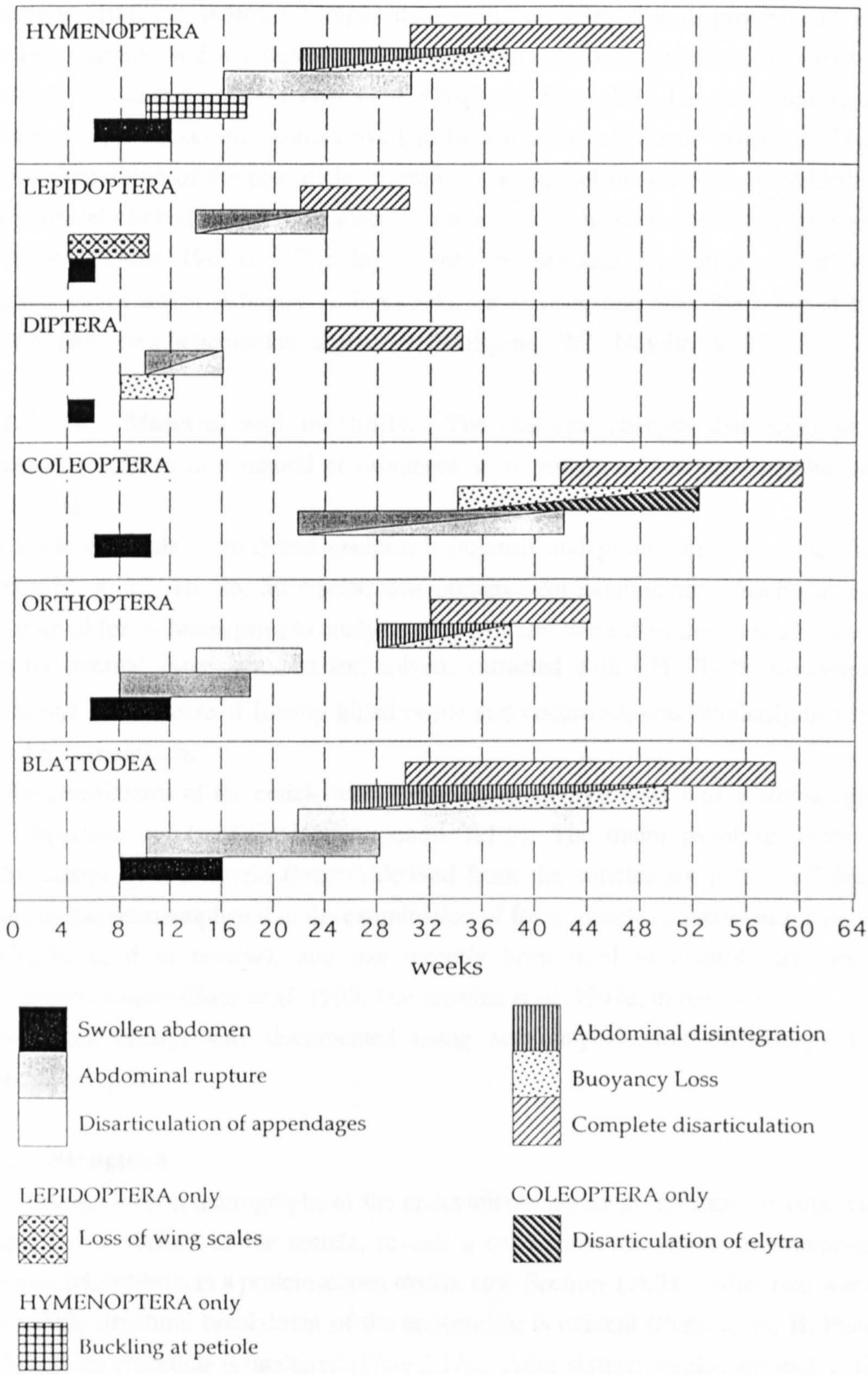


Figure 2.09 Summary of insect decay with time in the laboratory.

may be cross-linked with proteins via catechol and histidyl moieties in a strengthening process known as sclerotization (Kramer *et al.* 1995). The cuticle comprises an inner procuticle (10μm to 0.5mm) composed of chitin complexed with protein and a small amount of lipids, and a sculpted outer epicuticle (0.1-3μm) composed of cross-linked lipid and protein molecules (Evans 1984; Chapter 1, Fig.1.03). The procuticle is formed of two units, a thicker endocuticle overlain by a thinner sclerotized exocuticle (Richards 1978). The chitin of the procuticle is arranged in parallel microfibrils embedded within and intimately linked to a protein matrix. Layers of such microfibrils are arranged like plywood (Neville 1967a). The layers may be stacked one atop the other in a unidirectional fashion (Chapter 1, Fig.1.04), or stacked one atop the other at a slight angle to produce a helicoidal arrangement (Bouligand 1965; Neville 1970).

2.7.1.1 Material and methods. The chemical changes that occur in insect cuticle as it decays in a natural environment were monitored using a combination of techniques.

Cuticle of beetle (elytra) and cockroach (tegmen and pronotum) from each sample interval (2, 4, 12, 16, 26, 30 weeks) was prepared for examination. Each carcass was freeze dried for 24 hours prior to analysis. The cuticles were then mechanically separated from the internal tissue, crushed and solvent extracted with CH_2Cl_2 by ultrasonication (4x15min). The cuticle of freshly killed beetle and cockroach was similarily treated as a basis for comparison.

The constituents of the cuticle were analysed using Pyrolysis Gas Chromatography/ Mass Spectrometry (py-GC/MS) (Appendix A1.5). The major pyrolysis products of chitin (numbers) and protein (letters) derived from the cuticles are listed in Table 2.4. Pyrolysis has been employed in the examination of fossil cuticle (Stankiewicz *et al.* 1996, 1997a, b, c, d in review), and has recently been used to quantify the decay of stromatopod cuticle (Baas *et al.* 1995; Stankiewicz *et al.* 1997e, in review).

Structural change was documented using scanning electron microscopy (SEM) (Appendix A1.1).

2.7.2 Structure

Scanning electron micrographs of the endocuticule layers in the fresh insects, viewed parallel to the surface of the cuticle, reveals a solid mass known to be comprised of chitinous microfibrils in a proteinaceous matrix (see Section 1.4.2). After two weeks of decay, little structural breakdown of the endocuticle is evident (Plate 2.1A, B; Plate 2.2 A, D) and the epicuticle is unaltered (Plate 2.1A). After sixteen weeks, the endocuticular structure became looser and the fibres readily pull apart when it was fractured (Plate 2.1 C,D). Where the laminae are helicoidally arranged, the microfibrils display a 'florette-like' patterning (Plate 2.1 D). The epicuticle remains unaltered (Plate 2.1 C). After thirty weeks, the endocuticle showed an open meshwork of microfibrils that had begun to

unravel, as evidenced by the separation of fibres from the main mass (Plate 2.1 E.F). When decay progresses to sixty-five weeks, the intervening matrix has been entirely consumed, revealing the distinct microfibrils (Plate 2.3B). Where laminae are helicoidally-arranged, a basket-weave structure is revealed (see Plate 8.1). The epicutcle remains unaltered (Plate 2.3A). Bacteria were occasionally observed in scanning electron micrographs of the cuticle (Plate 2.1 E), and fungal hyphae were evident (Plate 2.3 C,D).

2.7.3 Chemistry

The pyrolysis of fresh an decayed insect cuticles yielded products which can be confidently assigned to two component biopolymers: chitin and proteins (see Section 1.4.3.2). Over the course of the experiment, the proportion of products derived from these macromolecules altered significantly. The most abundant pyrolysis products derived from the chitin biopolymer are (Fig. 2.11, 2.12, Table 2.4): acetic acid (1), acetamide (4) and the acetamido substituted furan (14). These compounds appear in the chromatograms as broad peaks due to their chemical nature and their relatively high abundance in the pyrolyzate. Acetic acid on its own is not a marker for chitin since it can derive from several sources including proteins and polysaccharides (Stankiewicz *et al.* 1996). Also important are acetyl and methyl substituted ethanylacetamides (9, 10, 10', 10''), pyrrolecarboxaldehyde (8) and pyridone (5) and amine (7) derivatives. While all of these products were identified in the freshly prepared cuticle, the majority of them became more abundant in the pyrolyzates of the decayed specimens. An increase in the abundance of pyrolysis products such as pyrrolecarboxaldehyde (8) and acetyl ethanylacetamide (10) were obvious in the most decayed samples, reflecting the degradation of the chitin-protein cross-links (Stankiewicz *et al.* 1996, 1997e, in review).

Protein moities are cross-linked with chitin and therefore pyrolysis is expected to yield products related to amino acids. Most of these pyrolysis products can be assigned to amino acids or even to particular short sequences in polypeptides (Table 2.4). The pyrograms of fresh cuticle show an overwhelming dominance of the pyrolysis products of proteins rather than chitin, which reflects the average chitin (40%) and protein (60%) content found in Coleoptera and Blattodea exoskeletons (Muzzarrelli 1977). Components such as pyrrole (a) and its alkylated homologues (c,d) are indicative of proline; toluene (b) and cyanobenzenes (g, h) are assumed to indicate the presence of phenylalanine. Tryptophan is indicated by the presence of methylindole (j), and tyrosine pyrolysis products include phenol (e). The abundance of these components decreased sharply with decay, a feature particularly evident in coleopteran cuticle (Fig 2.11). Apart from the markers of proline, phenylalanine, tyrosine and tryptophan, the pyrolysis of fresh cuticles yielded very distinctive components identified as 2,5-diketopiperazines ($DKP_{1,2,3}$) of proline alanine (pro-ala), proline valine (pro-val), proline arginine (pro-arg) or proline-glycine (pro-gly) (Munson and Fetterolf, 1987; Stankiewicz *et al.* 1996) (see also Section 8.6). The abundance of these components does not decrease markedly with decay in

insects, although they are known to breakdown very rapidly in other arthropods (*e.g.* crustaceans: Stankiewicz *et al.* 1997e, in review).

2.8 DISCUSSION

2.8.1 Introduction

Few experiments have been conducted previously upon the decay of terrestrial invertebrates (see Section 2.2). The results described here highlight the protracted period required for decay and disarticulation of terrestrial invertebrates compared to those in the marine environment. For example, in the experiments that Briggs and Kear (1994b) conducted upon shrimps, little remained of the carcass after ten weeks. In the laboratory experiments performed during the present study, little decay was evident within this period (see Fig. 2.10). Some marine organisms can be destroyed within days of the commencement of decay (Harding 1973). Insects on the other hand, may require five years for the complete disintegration of the exoskeleton (Seastedt and Tate 1981).

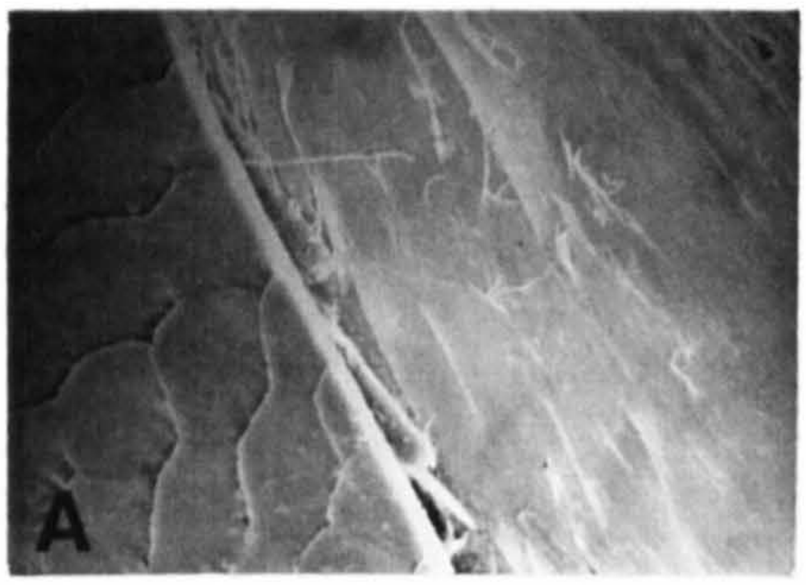
2.8.2 General decay

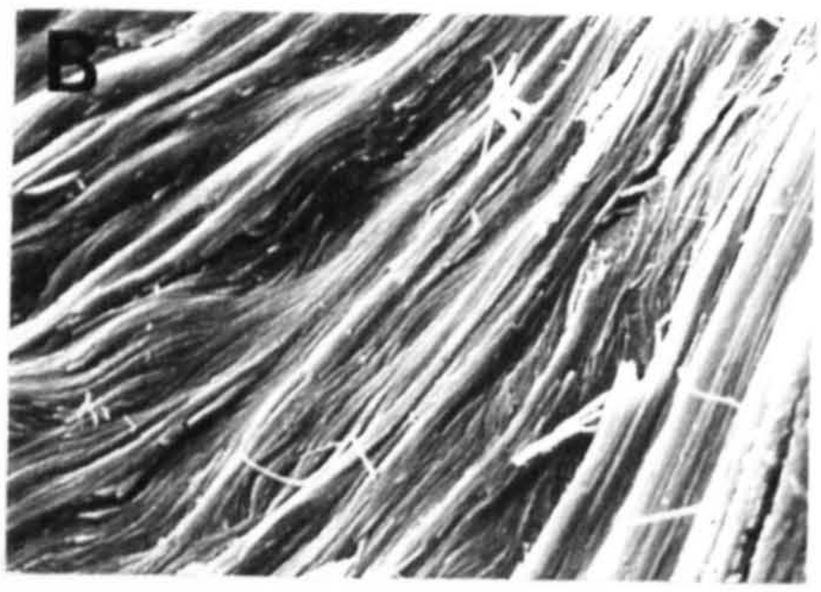
2.8.2.1 Laboratory experiments. The carcass of insects can persist for months with little external manifestation of decay (see Fig. 2.09). However, internal breakdown generally begins within days (Fig. 2.09). The smaller the specimen, the more rapid the completion of internal breakdown. The ganglion, ovaries/testes and salivary organs disintegrate within the first two weeks of decay. Body fats begin to breakdown within four weeks producing a cream coloured material that becomes increasingly brown with time. The partially sclerotized crop (see Neville et al. 1967) and gut can persist for lengthy periods (up to seven months in the cockroach) and are usually the only organs recognisable in any order by week four. Internal material usually leaks from the anal and genital openings.

In all orders, the initial effect of decay is a swollen abdomen (Fig. 2.09). This is noted in Lepidoptera and Diptera after only four weeks and all other orders by eight. The breakdown of internal material produces gas (predominantly CO_2). The decayed internal material slumps to the lowest point of the body, generally the ventral surface of the abdomen. A combination of these phenomena ultimately rupture the abdomen, either between segments (particularly T_6 and T_7) or along the tergite/sternite boundary. Internal material is quickly lost through these ruptures. The abdominal segments become progressively disarticulated.

The development of enshrouding microbial films and fungi on and within the carcass (Plate 2.3), are particularly important to the progress of disarticulation. Since they also create a micro-environment about the carcass, they may be important to internal decay (see Seilacher *et al.* 1985). Films begin to appear about the anus and genital openings with the leakage of internal material. Therefore the appearance of the films is controlled by the rate of decay of the carcass. In Diptera, Hymenoptera and Lepidoptera, the films

Plate 2.1 Decay of cuticle (Blattodea: tegmen) in natural setting. A & B, Cuticle after 2 weeks of decay. A, Exposed endocuticle (right) reveals indistinct lineation. x600. B, Fibres of the endocuticle. x900. C & D, Cuticle after 16 weeks of decay. C, Exposed endocuticle reveals initial stage of decay: fibres now distinct. x900. D, Fibres of the endocuticle, revealing distinct vacancies, and a 'florette'-like arrangement. x2250. E & F, Cuticle after 30 weeks of decay. E, Fibres of the endocuticle reveal distinct linear arrangement. Vacancies are now distinct. In places, bacteria may be seen adhered to the cuticle surface. x900. F, Vacancies of the endocuticle. x2250. All specimens were decayed under natural conditions during the winter/spring of 1996/97.


A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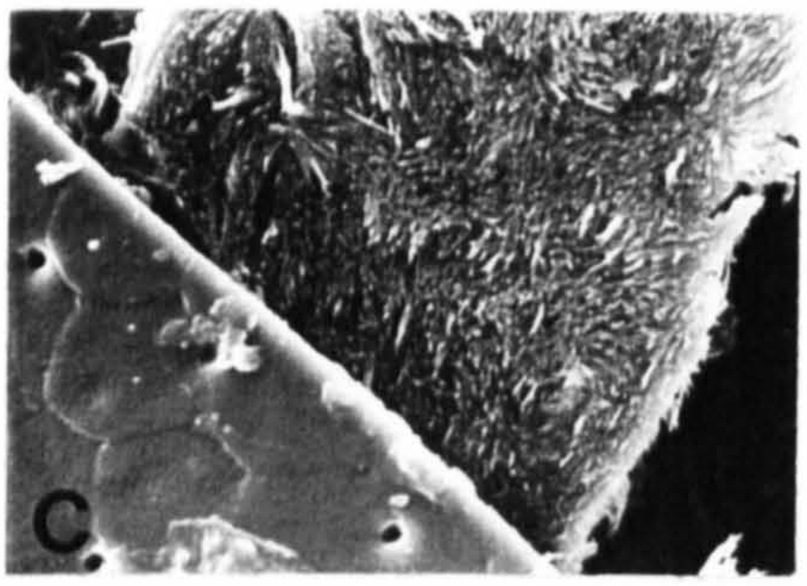
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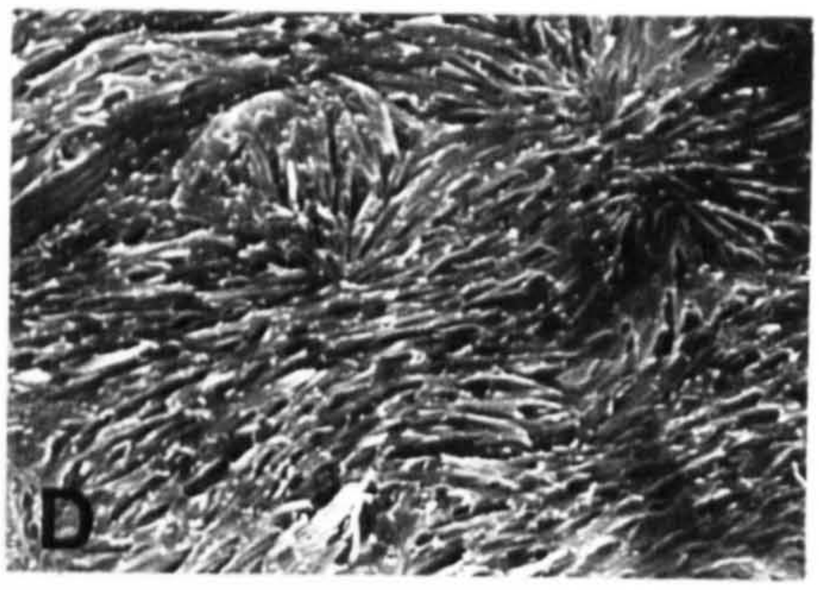
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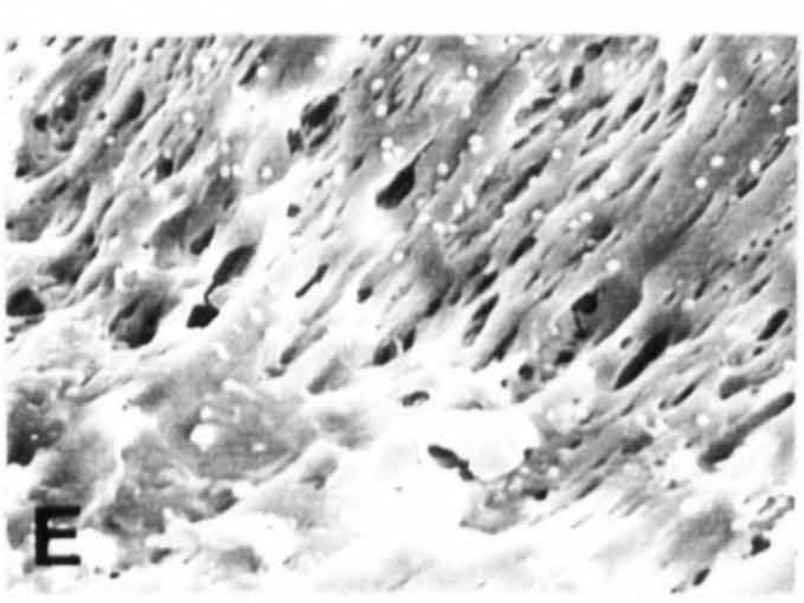
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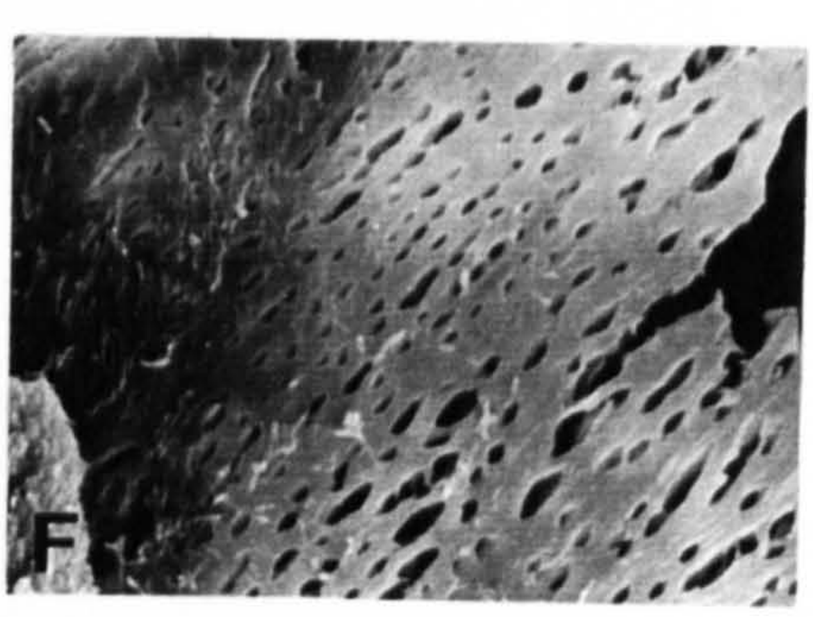
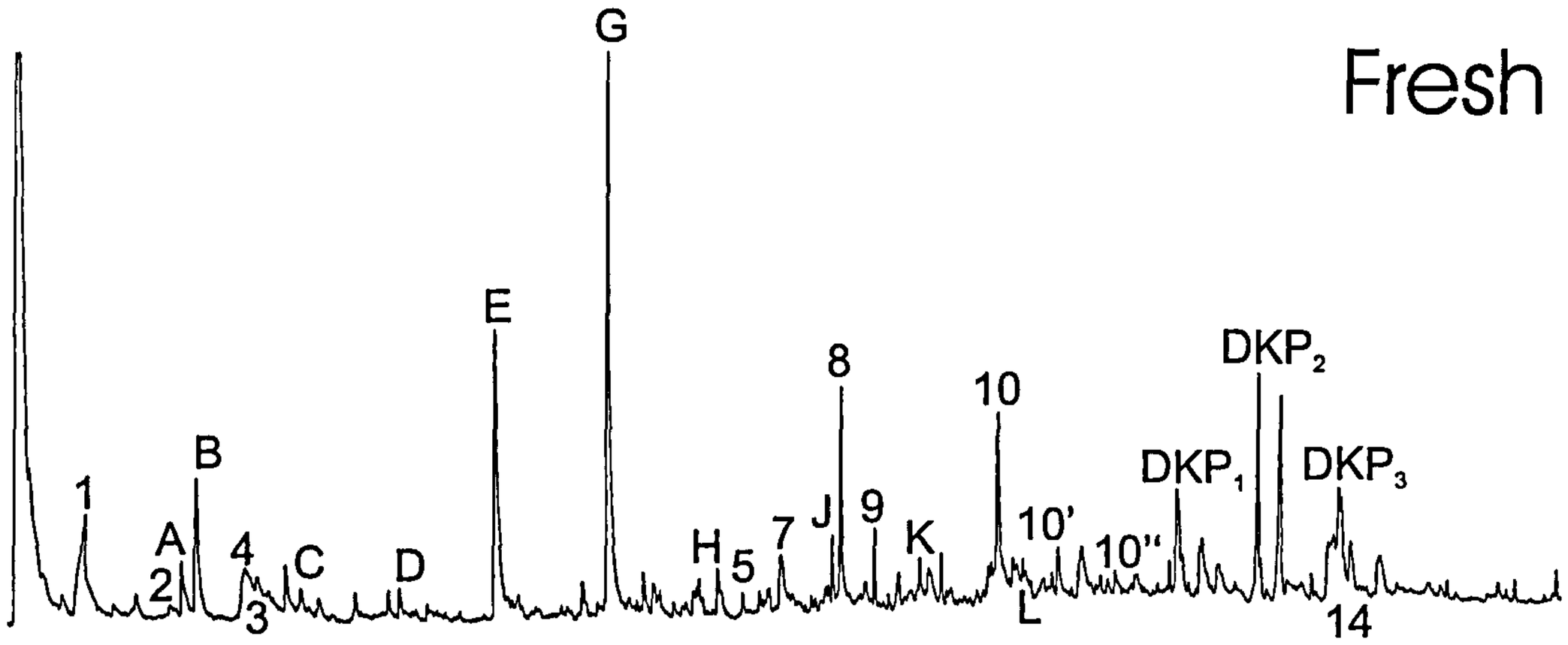
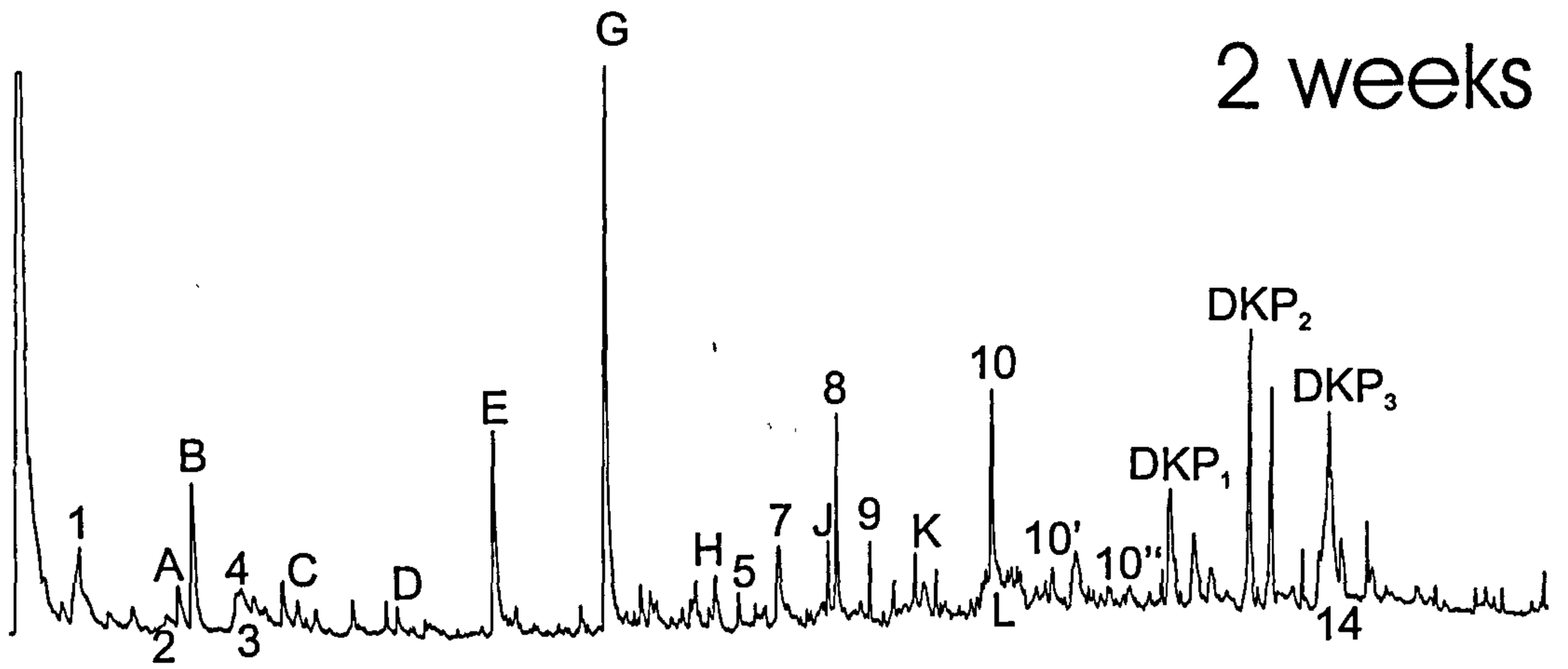

F

Figure 2.10 Reconstructed ion chromatograms (pyrolysis at 610°C for 10 sec) of the endocuticle of the elytra of the American cockroach (*Periplaneta americana*). Numbers indicate major pyrolysis products derived from chitin and letters those from amino acids (details in Table 2.4). DKP refers to pyrolysis products of proteins with 2,5-diketopiperazine structure.


Fresh
G
E
8
10
DKP2
B
DKP1
DKP3
1
A
4
C
D
H
5
7
J
9
K
10'
10''
2
3
L
14


2 weeks
G
E
8
10
DKP2
B
DKP1
DKP3
1
A
4
C
D
H
5
7
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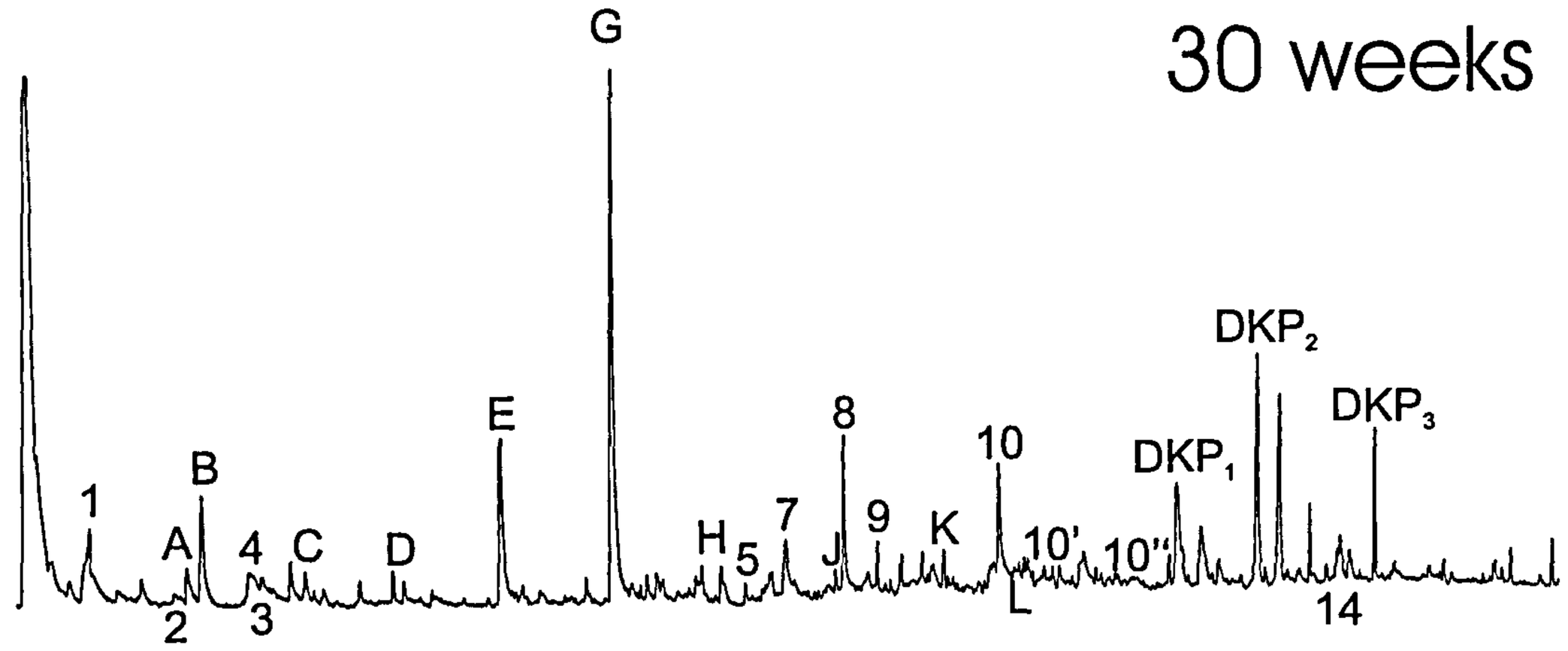
9
K
10'
10''
2
3
L
14


30 weeks
G
E
8
10
DKP2
B
DKP1
DKP3
1
A
4
C
D
H
5
7
J
9
K
10'
10''
2
3
L
14

Relative intensity
Retention time (1-55 min)

Peak*	MS characteristics	Compound name	Origin
(1)	<u>60</u>	Acetic acid	Chitin
(2)	<u>79</u>, 52	Pyridine	Chitin
(3, A)	<u>67</u>, 55	Pyrrole	Ch, Pro
(4)	59	Acetamide	Chitin
(5)	<u>93</u>, 66	Methylpyridine	Chitin
(6)	<u>109</u>, 81, 53	Methylpyridone or Hydroxypyridine†	Chitin
(7)	<u>107</u>, 79, 51, 78	2-Pyridinecarboxaldehyde [T]	Chitin
(8)	<u>127</u>, 42, 85	Acetylpyrrolidone[T]	Chitin
(9)	<u>137</u>, 109, 95, 81, 68, 53	Acetylpyridone	Chitin
(10, 10′, 10″)	<u>125</u>, 83, 54, 42, 53	3-Acetamidofuran††	Chitin
(14)	<u>204</u>, 59, 101, 114, 57	1,6-anhydro-2-acetamido-2-deoxyglucose†	Chitin
(A)	<u>67</u>, 55	Pyrrole	Ch, Pro
(B)	<u>92</u>, 91	Toluene	Phe
(C)	<u>81</u>, 80, 52, 50	C_1-pyrrole	Hpro
(D)	<u>104</u>, 78, 51, 103	Styrene	Phe
(E)	<u>95</u>, 94, 66	C_2-pyrrole	Hpro
(G)	<u>108</u>, 107, 77, 79	3- and 4-methylphenol	Tyr
(H)	<u>120</u>, 91, 65	Vinylphenol	Tyr
(J)	<u>131</u>, 130, 77	C_1-indole	Trp
(K)	<u>168</u>, 70, 44, 97, 125	2,5-diketopiperazine	Pro-Ala
(L)	<u>154</u>, 41, 83, 111, 70	2,5-diketopiperazine	Pro-Gly
($DKP_{1,2,3}$)		2,5-diketopiperazine	Pro-Val
			Pro-Pro

*Numbers in parentheses refer to peaks on the chromatograms (Figure 2.11)

[T] Based exclusively on interpretation of mass spectra and NIH mass library

† Follow van der Kaaden *et al.* 1984; †† Follow Franich *et al.* 1984.

Table 2.4 List of major chitin and protein pyrolysis products recognised in the pyrolysates of modern insect cuticles. Masses in bold indicate base peak and masses underlined indicate molecular weight (MW).

Plate 2.2 Decay of sclerotized cuticle (Coleoptera: elytra) in natural setting. A & B, Cuticle after 2 weeks of decay. A, Layers within the cuticle. Indistinct lineations apparent. x400. B, Linear arrangement of fibres. x1500. C & D, Cuticle after 30 weeks of decay. Internal layers of cuticle revealing distinct vacancies. x400, x1500. All specimens were decayed under natural conditions during the winter/spring of 1996/97.

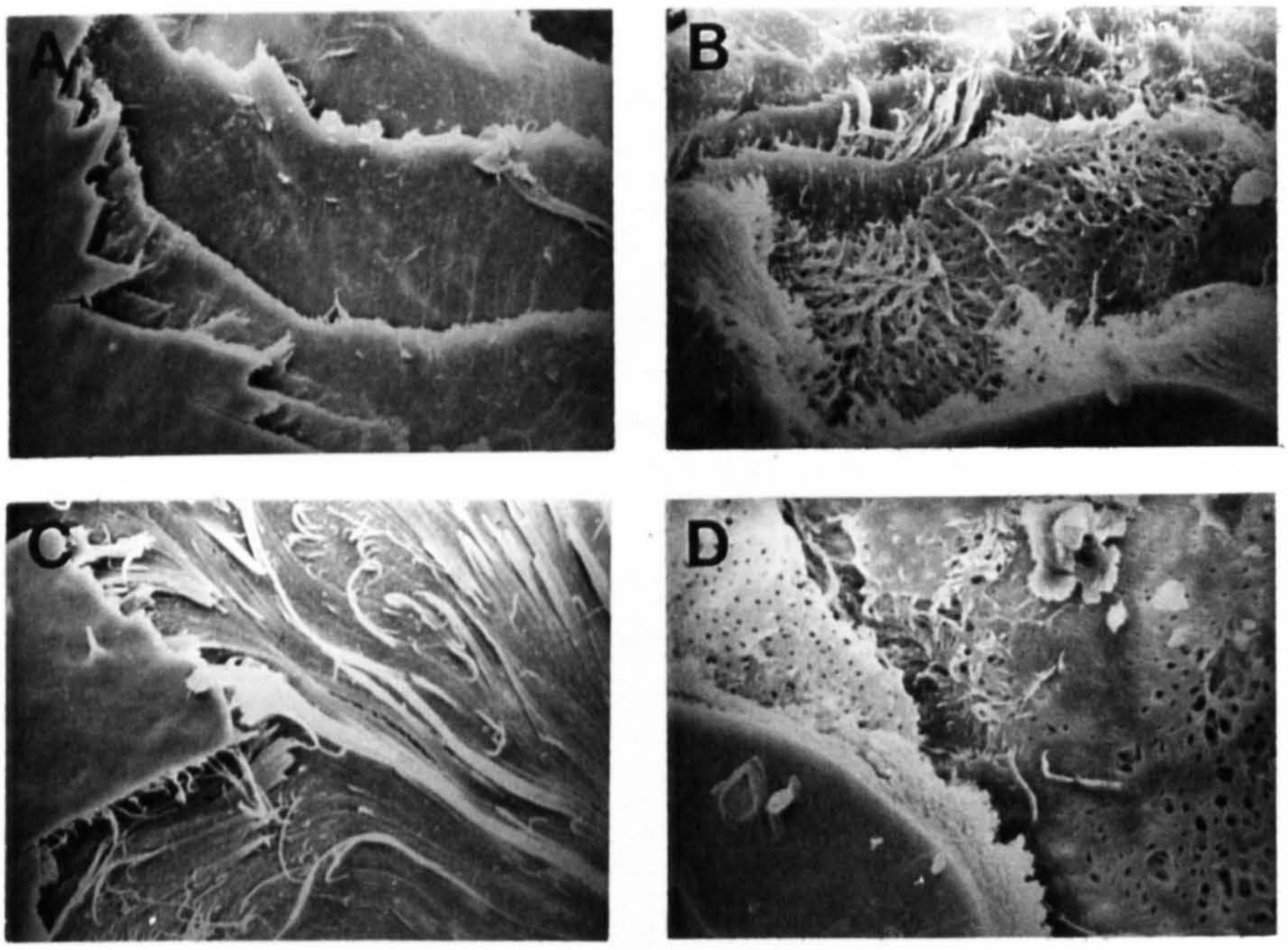
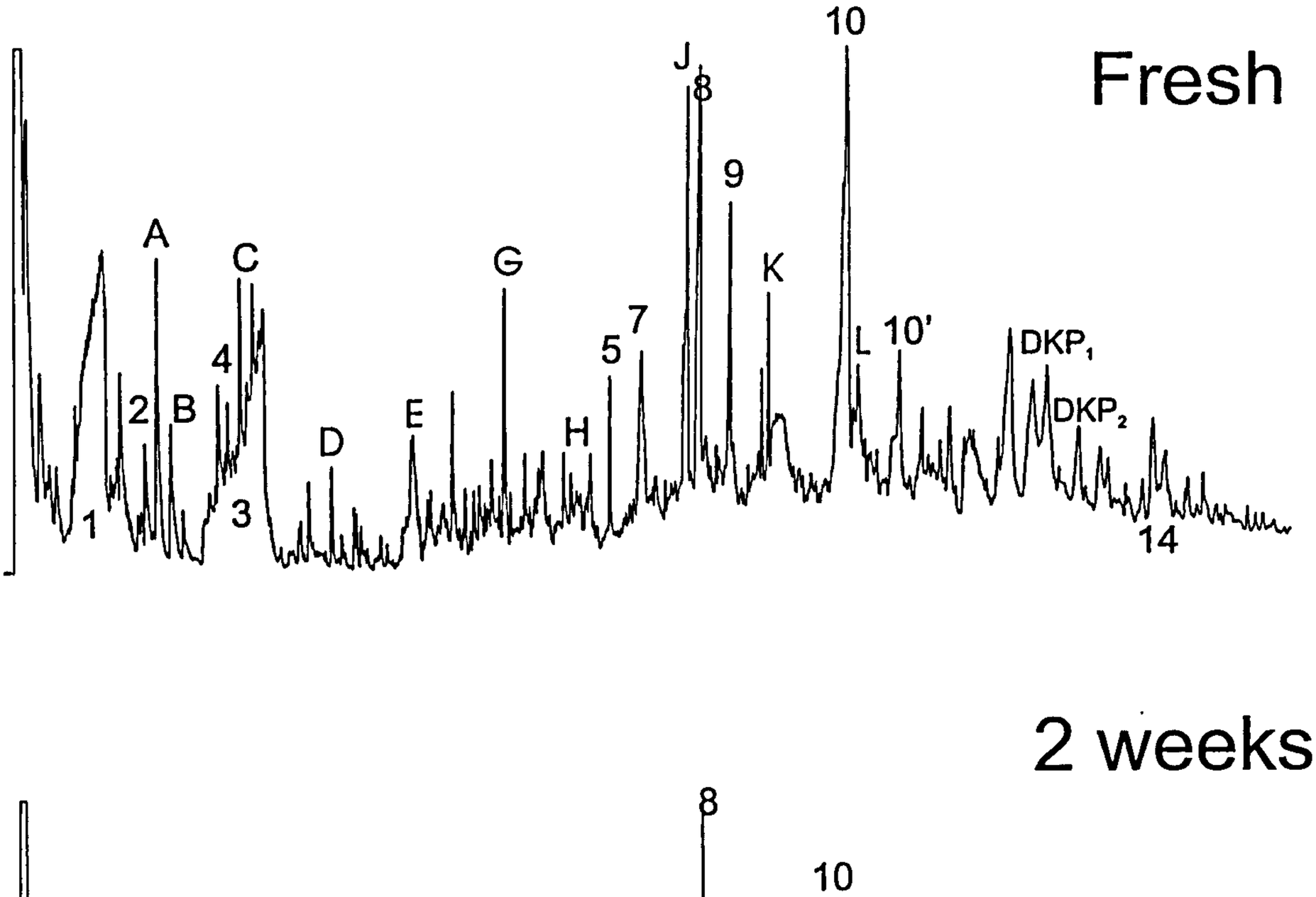
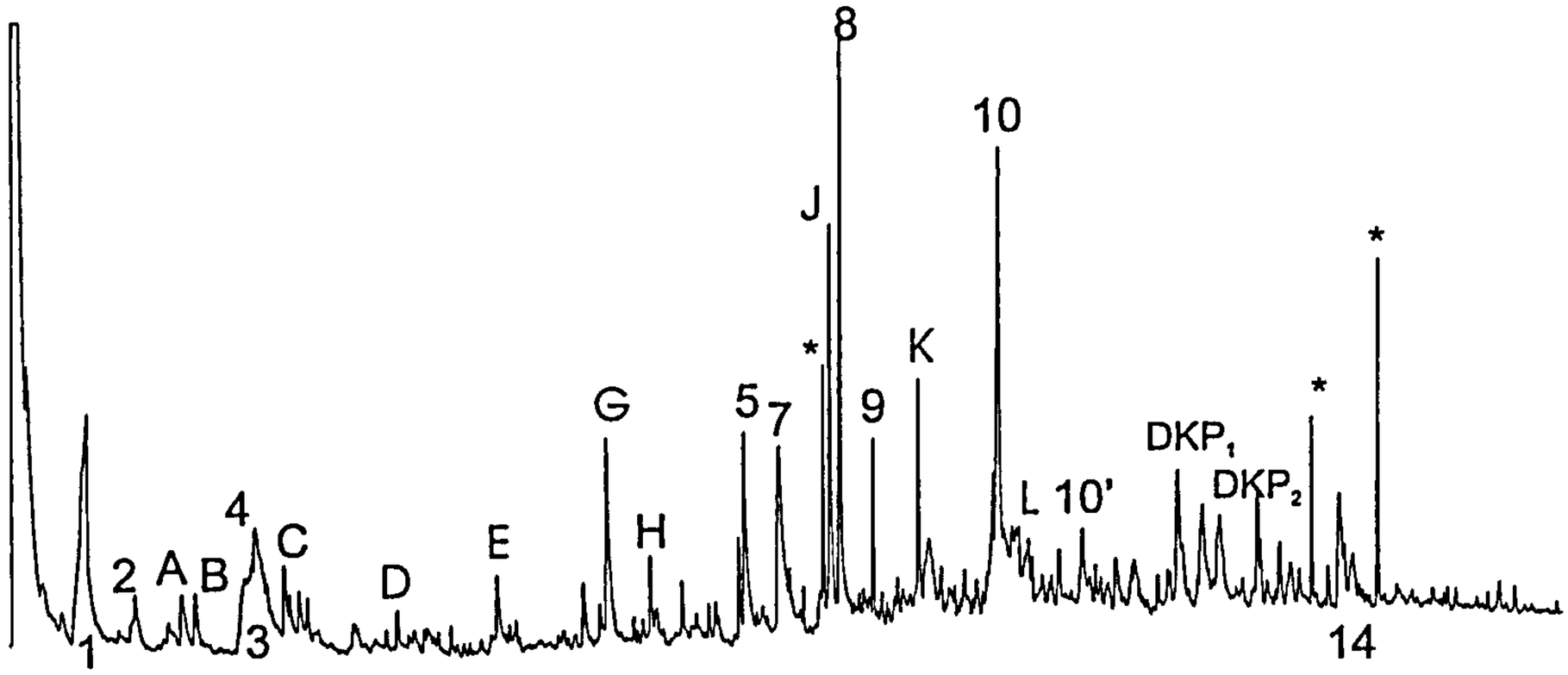

A
B
C
D

Figure 2.11 Reconstructed ion chromatograms (pyrolysis at 610°C for 10 sec) of the endocuticle of the elytra of the mealworm beetle (*Tenebrio molitor*). Numbers indicate major pyrolysis products derived from chitin and letters those from amino acids (details in Table 2.4). DKP refers to pyrolysis products of proteins with 2,5-diketopiperazine structure.


Fresh
1
A
2
B
3
4
C
D
E
G
H
5
7
J
8
9
K
10
L
10'
DKP1
DKP2
14


2 weeks
1
2
A
B
3
4
C
D
E
G
H
5
7
8
J
*
9
K
10
L
10'
DKP1
DKP2
*
14

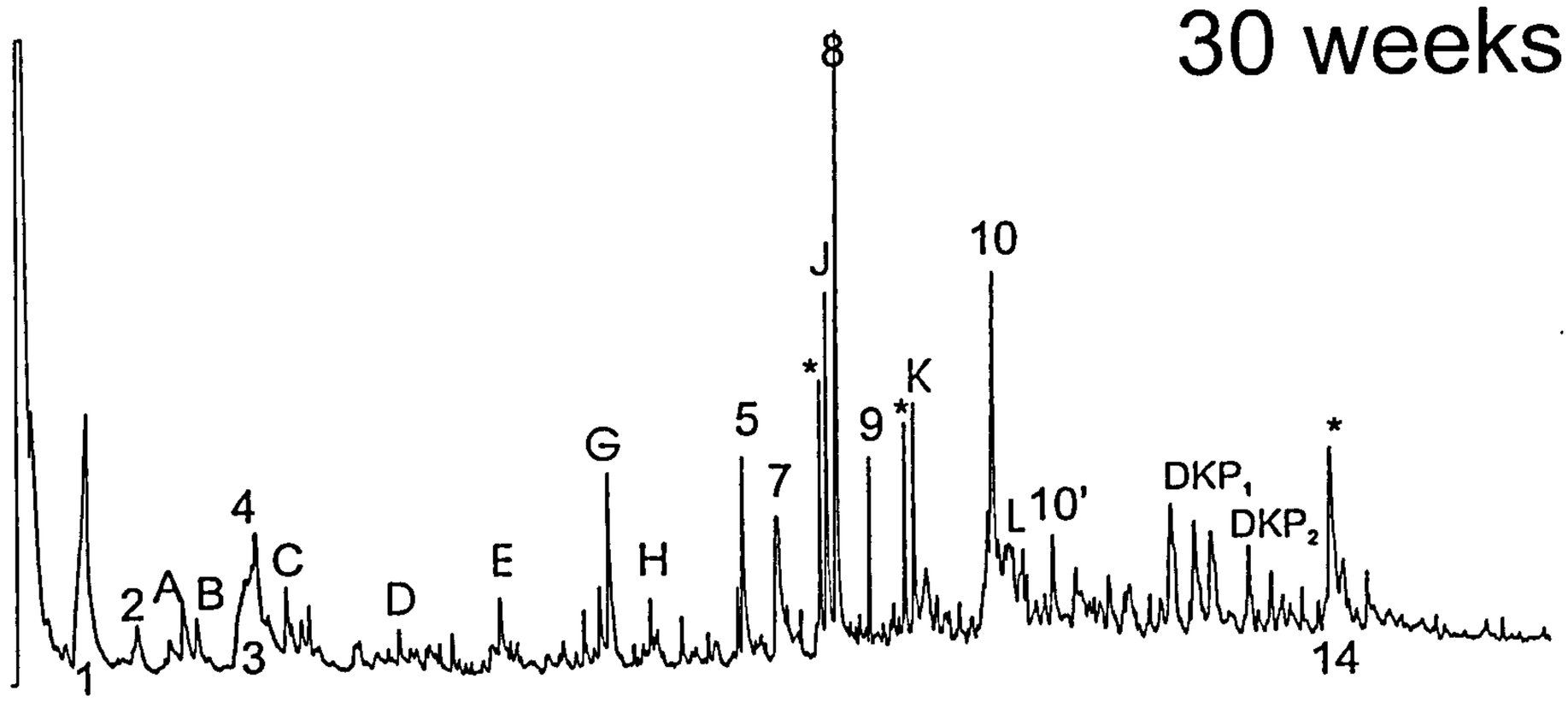
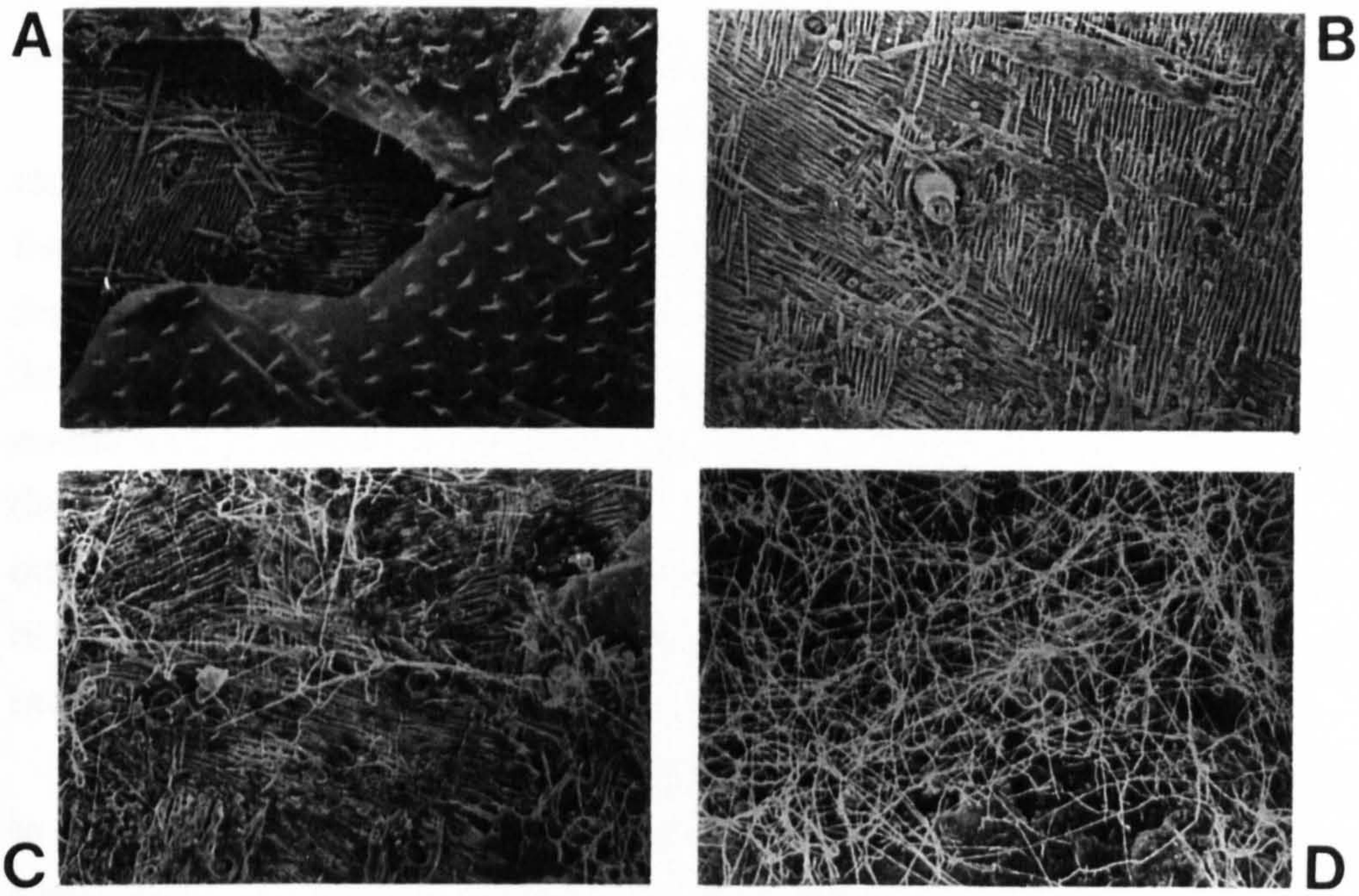

30 weeks
1
2
A
B
3
4
C
D
E
G
H
5
7
8
J
*
9
*
K
10
L
10'
DKP1
DKP2
*
14

Plate 2.3 Decay of cuticle (Coleoptera: elytra) in laboratory setting. All specimens have experienced 65 weeks of decay. A, Break in unaltered epicuticle reveals basket-weave arrangement of chitin-microfibrils. x325. B, Basket-weave arrangement of chitin microfibrils. x350. C, Fungal hyphae partially covering decayed endocuticle. x300. D, Fungal hyphae growing about decayed cuticle. x400. All specimens were decayed under laboratory conditions in fresh water at 25°C.


A
B
C
D

appear by around week eight and quickly enshroud the carcass. In Orhtoptera, films are noted after fifteen weeks and in Blattodea and Coleoptera after twenty. The ventral surface is rapidly covered, and the legs enshrouded. The films thenceforth control disarticulation. Limbs are frequently observed detached from the thorax, but held in position by the film. The abdomen, frequently reduced to a loose assemblage of tergites and sternites, may also be held together by the enveloping film. If the film becomes dense enough it may contribute to a loss of buoyancy. However, these cohesive films may adhere to any surface film, prolonging the residence time on the surface.

Disarticulation of appendages is highly variable. The antennae generally disarticulate rapidly and frequently remain on the surface. The mouth organs often remain articulated throughout the experiment, ultimately matted to the head. Disarticulation of the cerci and female ovipositor generally precede the disarticulation of the posterior abdomen (see Fig. 2.09). Disarticulation of the legs generally progresses from tarsus to thorax. The legs of orders with prominent metathoracic legs (*e.g.* Blattodea and Orthoptera), often detach at the coxae. The larger the leg, the more likely it is to detach as a single unit. The legs of other orders may disarticulate at the trochanter. Each leg behaves independently of the others, and it is common to have some legs disarticulated while the other legs remain intact. Detachment of the legs always precedes detachment of the wings.

The wings are generally the last appendage to detach, frequently remaining articulated to the thorax when all else has disarticulated (see Fig. 2.09). In the case of the Lepidoptera, the scales of the wings are quickly lost, and the wings reduced to spoke-like veins within a matter of weeks. The Blattodea generally lose the clavus (anal region) of the tegmen before disarticulation from the thorax. In the case of the Orthoptera, the wings generally adhere to the torso, precluding continued disarticulation. In all cases, bar Coleopteran, the wings experience venational splitting during the course of decay, and are ultimately fragmented. Coleopteran elytra disarticulate as a unit and remain intact.

While wing size to body ratio is an important control on residence time on the surface (see Martínez-Delclòs and Martinell 1993), more important is the position of the wings. For example, lepidopterans with outspread wings remain on the surface throughout their prolonged disarticulation. Lepidopterans with wings shrouded about the body, on the other hand, descend to the bottom after between fourteen and twenty-four weeks. Wings folded about the body also exert another important control - they trap air so aiding buoyancy. This is particularly important in the orders Blattodea, Orthoptera and Coleoptera. Trapped air beneath the outer wings also aids survival during transportation (Chapter 3).

Disarticulation of the head always occurs at a late stage. The thorax is generally the last component of the body to disarticulate. The size of the insect may affect surface residence time. Ants (Hymenoptera) which lack wings remain on the surface for extended periods because the weight of the specimen is rarely enough to break the

miniscus. Descent to the bottom normally requires the additional weight of a microbial film.

2.8.2.2 Field experiments. The results of the pond experiments are directly comparable to those of the laboratory in all but duration and timing of events. The only significant difference is in the timing of events (Fig. 2.10). The field-based experiments took place during the winter and spring months (average water temperature 6°C), decay was more rapid than the laboratory experiments. This can almost certainly be attributed to the presence of decomposing organisms. Nematodes were noted intimately associated with the internal soft tissue of a number of specimens. Several cockroach carcasses were missing, holes having been nibbled in the muslin. Both small fish and tadpoles were observed in the pond and may have been responsible. Other micro-organisms were observed in the soft tissue, although identification was not possible. Fungi associated with the insect carcasses may also have increased the rate of decay.

Initial internal decay of the laboratory specimens must have resulted from the activity of the gut bacteria. The bacteria of the inoculum would only have gained entry following a rupture of the integument - a relatively slow process (see Fig. 2.09). However, drowning of the specimens in the pond would have ensured a rapid penetration of the carcass by the pond bacteria which may have hastened decay. Enforced submergence (considerably in advance of its natural occurrence), necessitated by the nature of the field experiments, may also have played an important role. Once disintegration of the carcass has begun, the fragmented insect would decay more rapidly (see Chan 1970 and Plotnick 1986 for experimental analogues).

2.8.3 Order-specific decay

All insect orders pass through a broadly comparable decay sequence, though they differ in the timing of particular events (Fig. 2.09; 2.10).

2.8.3.1 Diptera and Lepidoptera. The lightly sclerotized orders Lepidoptera and Diptera decay at comparable rates. The significant difference between them can be attributed to the difference in wing span. The large wings of the Lepidoptera ensures that decay occurs predominantly on the surface. The Diptera, with a smaller wing span, rapidly lose buoyancy and disintegrate on the vessel bottom. The lepidopteran scales (modified hairs), which cover much of the body, are shed during the early stages of decay. The body hairs of the bristly Diptera are shed over a more protracted period.

2.8.3.2 Blattodea and Orthoptera. The orders Blattodea and Orthoptera display comparable decay sequences, with decay more protracted in the former. While the onset of the initial stages of decay (abdominal swelling and rupture) is comparable, rupture of the abdomen is delayed in the blattoids. This may reflect the greater size range

in the blattoid specimens; the larger (>2.5cm) blattoids rupture before the smaller (<2.5cm) ones.

Other marked differences include the timing and manner of leg loss, and the nature of wing disarticulation. The metathoracic legs are the largest appendages in orthopterans and consequently detach intact at the coxae, well before the pro- and mesothoracic legs disarticulate in a more irregular fashion. The metathoracic leg is also usually the first to detach in blattoids but this is not always the case. Since all the legs in blattoids are of similar size, disarticulation progresses in a more random fashion.

The wings of both orders remained attached for much of the experimental run. Blattoid wings, albeit without the clavus and with ragged margins, frequently remain attached to the thorax long after everything else has become detached. Orthopteran wings, on the other hand, become detached and only remain associated with the body due to microbial cohesion. Orthopteran wings fold around the body, thus facilitating microbial bonding. Even manual manipulation cannot remove the wings from the carcass intact.

2.8.3.3 Coleoptera. The decay sequence of Coleoptera is more distinctive than those of the other orders studied. Swelling of the abdomen occurs at a similar rate to that in other orders, but it is frequently obscured by the elytra. However, rupture of the abdomen was slow. When the abdomen has completely disarticulated, the sternites still remain attached together forming a 'plate'. The smaller legs also disarticulate more slowly and frequently remain intact even after the loss of buoyancy. The elytra commonly trap air beneath them, prolonging residence time at the surface. Submergence generally only occurs when the elytra detach. Colour loss is usually the only sign of decay of the elytra.

2.8.3.4 Hymenoptera. The small size of the specimens ensures a protracted residence at the surface. The specimens always 'buckle' at the petiole. The abdomen swells rapidly exposing the arthrodial membrane between the segments but this does not rupture until late in the decay sequence. Disarticulation of the appendages progresses from distal to proximal. The scape of the antennae generally remains articulated to the head throughout the experiment. Submergence of the carcass is usually dependent upon the added weight of the enshrouding microbial films.

2.8.4 Cuticle decay

The decay of arthropod cuticle in marine water has been the subject of two recent studies that have shown that as the cuticle decays, chitin is selectively preserved (*Crangon crangon*: Baas *et al.*1995; *Neogonodactylus oerstedii*: Stankiewicz *et al.* 1997e, in review). The decay of arthropod cuticle in freshwater and terrestrial environments, however, is poorly documented (Stankiewicz *et al.* 1997a). Only the evidence of fossil

insects indicates that in insect cuticle, chitin survives preferentially while protein decays (CHAPTER 8; Stankiewicz *et al.* 1997b, c; McCobb 1997).

This investigation has shown that significant chemical and structural decay of insect cuticle is evident after 15 weeks. The protein component of the endocuticle (proline, phenylalanine, tyrosine and tryptophan) decays readily, such that by week 30, the cuticle pyrolyzates are dominated by chitin-derived products (Fig. 2.10, 2.11) all of which can be readily identified in the fresh cuticle. Even after sixty-five weeks, the chitinaceous microfibrils are evident although the intervening proteinaceous matrix has decayed (Plate 2.3A, B). The decay of the protein component is reflected in the vacancies of the endocuticle which increase in size as the protein component decays, revealing a loose meshwork of chitin microfibrils (Plate 2.1 C-F, 2.2 C, D, 2.3 A, B).

While the endocuticle experiences marked decay, the epicuticle does not show any evidence of structural breakdown (see Plate 2.3 A, B). This may reflect the hydrophobic nature of the outer cuticular layer (Kolattukudy 1976). The epicuticle, therefore, has more opportunity to be fossilized. Indeed, it is often preserved intact in fossils, even where the endocuticle has experienced decay or complete destruction prior to fossilization (*e.g.* CHAPTER 6, Plate 6.7).

Sclerotization plays an important role in the biochemical decay of cuticle. The difference in the decay of the cuticles of cockroach tegmen (Fig. 2.10) and beetle elytra (2.11) is clearly evident, as the leathery and flexible cuticle of the cockroach displays a more restricted protein decay than the rigid and brittle beetle cuticle. The exact nature of the biochemical control is currently the subject of a study at Bristol University.

The breakdown of insect cuticle is considerably more protracted than that of the crustacean (Baas *et al.* 1995; Stankiewicz *et al.* 1997e, in review). After two weeks, the matrix of the crustacean endocuticle has begun to decay, revealing a fabric of microfibrils. This corresponds with a marked decline in the abundance of protein markers in the pyrolyzate (Stankiewicz *et al.* 1997e, in review). The distinctive 2,5-diketopiperazines have also decreased to a negligible level by this stage. However, after two weeks of decay, insect cuticle displays only minor evidence of structural and chemical breakdown (Fig 2.10, 2.11). Indeed after thirty weeks all the markers detected in the fresh cuticle are still readily identifiable. Even after sixty-five weeks, the chitinaceous microfibrils are evident although the proteinaceous matrix is absent (Plate 2.3A, B). This survival of insect cuticle is almost certainly responsible for the extensive insect fossil record, providing a greater opportunity for fossilization (see CHAPTER 9).

CHAPTER 3

ACTUALISTIC EXPERIMENTS: TRANSPORT

3.1 INTRODUCTION

The degree of disarticulation, abrasion and fragmentation of animal carcasses is often related to the nature and distance of transport in the sedimentary environment (Allison 1986). However, predation (Trewin and Welsh 1976), sediment compaction (Shinn *et al.* 1977) and decay *in situ* (Briggs and Kear 1993a, b, 1994, 1995; Martínez-Delclós and Martinell 1993) can produce similar end products. Therefore a rigid application of the relationship between distance of transport and disarticulation can be misleading. Recent experiments (Allison 1986) have questioned the assumption that the preservation of complete carcasses and delicate appendages is indicative of limited transport (see Stürmer and Bergström 1973; Whittington 1971; Jarzembowski 1989; Todd 1991).

Cockroaches (Blattodea) represent some 80% of all known Upper Carboniferous insects (Carpenter and Burnham 1985). The vast majority of specimens (~90%) consist only of isolated wings or wing fragments (Carpenter 1992). Explanations for this preservational phenomenon have been varied: transport (Jarzembowski 1989); decay (Scudder 1886; Carpenter 1992); predation (North 1931; Todd 1991); trapping at the thermocline (Margalef 1983; Martínez-Delclós and Martinell 1993); and the difficulty of distinguishing small (non-wing) fragments on bedding planes crowded with plant fragments similar in appearance, particularly after diagenesis (Bolton 1921-1922; North 1931).

3.1.1 Aims and scope of work

Although cockroach tegmen are the most common fossils recovered from most Carboniferous deposits (Carpenter and Burnham 1985) most museum collections of such material are highly biased. In order to assess the taphonomy of a given biota it is imperative that all fossil material, regardless of completeness, is examined. However, many collections contain only the more intact or impressive specimens, with the remainder of the material either discarded or never collected in the first place. The most complete collection of fossil cockroaches is that gathered from the Writhlington Geological Nature Reserve, S.W. England.

In order to assess the taphonomic importance of decay (see Chapter 2) and transportation, a series of actualistic experiments was designed to provide quantitative

information on the relationship between skeletal durability and decay in modern cockroaches. Since modern blattoids are almost indistinguishable from those of the Palaeozoic (Carpenter 1992), the results can be applied specifically to the cockroaches of Writhlington.

3.1.2 Previous studies

The utility of experiments in interpreting fossils by replicating the conditions of mechanical disarticulation is now firmly established (see Briggs 1996, for review). To date, the primary focus of such experiments has been the abrasion and disarticulation of biomineralised shells, tests and other skeletal elements (*e.g.* molluscs, Chave 1964, Glover and Kidwell 1993, Daley 1993, Lutz *et al.* 1994; brachiopods, Sheehan 1978; echinoids, Kidwell and Baumiller 1990, Greenstein 1991; foraminiferans, Kotler *et al.* 1992; vertebrates, Korth 1979, Behrensmeyer 1975, 1982, Badgley 1986, Meyer 1991, Cook 1995b). The exception is the work of Allison (1986) who conducted disarticulation experiments on soft-bodied polychaetes and crustaceans using a tumbling barrel. His conclusion, that freshly dead specimens could be transported for considerable distances without disarticulation, has significant implications for the interpretation of the conditions under which exceptional preservation of fossils occurs (*e.g.* Burgess Shale). Rate of decay therefore has a significant effect upon the degree of disarticulation induced by transport. Carcasses which experience no decay prior to transportation are capable of withstanding lengthy journeys intact while, those which have begun to decay, disarticulate more rapidly the more decay they have experienced (Allison 1986).

Hitherto, taphonomy experiments have utilized tumbling barrels (although see Cook 1995b). However, sedimentological research during the 50s and 60s by Keunan (1956) indicates that such apparatus may not provide an adequate representation of the processes operating in natural fluvial systems. Material in a tumbling barrel tends to remain at the bottom of the cylinder, where, in the absence of bed load, it is abraded only by the passage of the cylinder walls. While the presence of baffles on the interior wall reduces this effect, it introduces a highly artificial bashing of the carcass. For a full discussion of the defects of this method, see Keunan (1956). Consequently the experiments described below employed a flume based upon Keunan's design (Fig. 3.01), which addresses some of the flaws inherent in tumbling barrels.

3.2 ACTUALISTIC EXPERIMENTS

3.2.1 Introduction

Transport is a commonly invoked, though rarely tested, explanation of fossil fragmentation. The following experiments were designed to quantify the effect of decay on the skeletal durability of the cockroach in a 'fluvial' environment.

3.2.2 Material and Method

Experiments were conducted upon the cockroach, *Periplaneta americana*, "the cosmopolitan, nocturnal, malodorous, disease-carrying, refuge-seeking, peri-domestic roach" (Gullan and Cranston 1994 p220; Chapter 2). Only live adult specimens were selected (n=30).

A series of experiments to assess the decay of the cockroach (Chapter 2), and to simulate the transport and disarticulation of fresh and decayed specimens, was performed under controlled conditions. The conditions of decay are described in Chapter 2.

Transport experiments were carried out in a circular flume (Fig. 3.01). Water movement is produced by two rotating paddles driven by an electric motor, which when run at 20Hz, produces a water velocity of ~1.0ms^{-1}. Calibration of the flow regime using a buoy allowed the distance travelled to be estimated, although the longer the experimental run, the more inaccurate was this figure.

The cockroaches were introduced into the flume in three batches: alive (n=10), after reaching decay state 1 (n=10), or decay state 2 (n=10) (see Chapter 2), by dropping them from ~10cm above the water. Cockroaches are introduced live because drowning is a better proxy of the likely mode of death in fluvial environments (see Martinez-Delclòs and Martinell 1993). The decayed specimens were terminated by suffocation, as detailed in Chapter 2. Following death, the behaviour and disarticulation of the drowned cockroach was comparable to that of the suffocated cockroaches.

The fate of each carcass was documented in a manner similar to the experiments of Chapter 2. However, in these transportation experiments the carcass was re-introduced into the flume after examination, and the experiment continued until the next state was reached. The process was repeated until the carcass had completely disarticulated. Recovery of the fragmentary specimen and its constituent parts became progressively more difficult during advanced disintegration, and the fate of the smaller disarticulated fragments often could not be determined.

3.2.3. Disarticulation sequence

Live cockroaches introduced to water are adept at avoiding drowning. In still water, they propel themselves across the surface by raising their body and agitating their wings (and will ultimately escape if conditions allow). In turbulent water, the cockroach assumes a survival position, curling its legs beneath its body and trapping air beneath its folded wings, to aid buoyancy. This stable orientation is maintained even under the most turbulent of conditions for periods of up to eight hours (the equivalent of 30km transportation), and for considerably longer under a more gentle flow regime. If the water is stilled, the cockroach will slowly recover its faculties and attempt to escape. Ultimately, however, the animal loses its stability and begins to roll. Estimation of time of death is hampered by the extended period of dormancy that precedes it, but was deemed to have taken place when appendage twitching ceased. The appearance of the

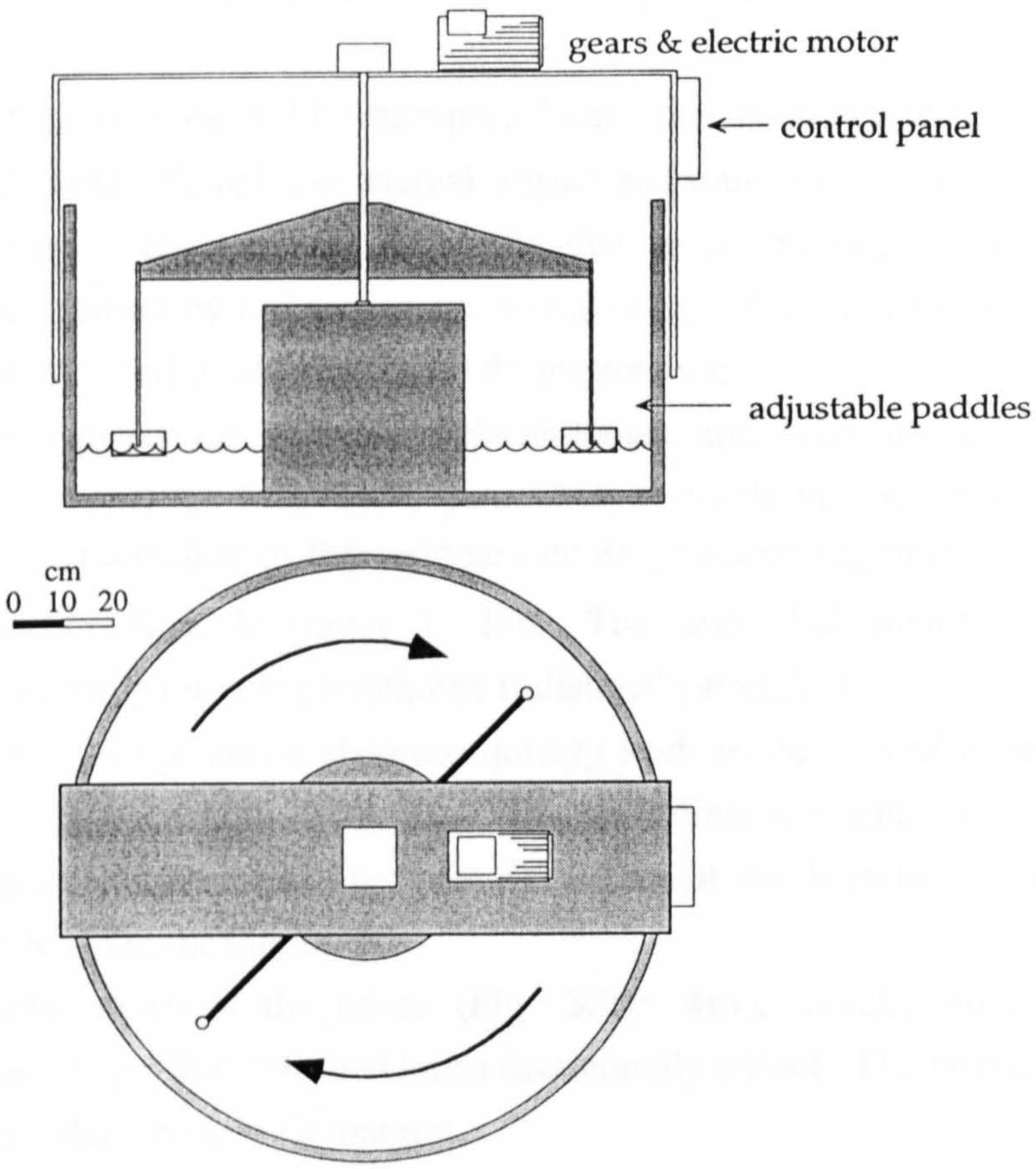


Figure 3.01 Rotating flume tank. (Modified from Kuenen 1956; Cook 1995).

body is unaffected by death (the effects of water uptake are not evident), which was presumably due to asphyxiation after obturation of the stigmata by water (see Baudoin 1976).

Carcasses introduced into moving water disarticulate in a series of stages similar to those in still water (see Chapter 2). The time taken to reach each disarticulation state is strongly influenced by the duration of decay prior to introduction into the tank (Fig. 3.04).

The initial stage reached by transported carcasses is similar to the first stage of decay (Fig. 3.02: **1m**) although the internal organs and musculature remain intact, if distinctly water logged. The limp appearance is due to a straining of the musculature and membrane induced by turbulence, not to the decay of internal tissue. At this stage, the tegmina involuntarily fold and unfold during rotation.

Rupture between the segments of the abdomen, and along the lateral margins, is rapid under transport (Fig. 3.02: **2m**), particularly towards the posterior, and may lead to complete disarticulation of the abdomen or its posterior segments (between T_6 or T_7). With disarticulation, buoyancy is lost. The arthrodial membrane connecting the head/thorax and pronotum/pterothorax is distinctly stretched.

The loss of the posterior abdomen quickly leads to the loss of internal tissue, leaving an empty cuticle sac (Fig. 3.02: **3m**). The abdominal segments disarticulate further into their tergites and sternites. The antennae detach at the fenestra. The legs, however, remain attached to the thorax.

The legs detach at the coxae (Fig. 3.02: **4m**), usually commencing with the metathoracic legs. The detached limbs occasionally refloat. The tegmina and hind wings show minor damage to their margins.

The thorax disarticulates between the meso- and metathoracic segments (Fig. 3.02: **5**). The wings remain attached to their respective segment, while the head/pronotum disarticulates from the mesothorax. The wings begin to split particularly along the three primary veins (media, costa and cubitus; Fig. 3.03). The clavus frequently disarticulates along the cubitus posterior vein (Fig. 3.03). Cross vein splitting is also noted.

Ultimately, the tegmina and hind wings detach from their respective segments. Splits continue to propagate along the three major veins of both the tegmina and the hind wings.

3.2.4 Discussion

There is a clear difference in the pattern of disarticulation of specimens introduced into the flume live and those which have experienced decay (Fig 3.04). However, there is little to distinguish the pattern in specimens introduced after decaying to stage 1 from those that have decayed to stage 2. Decayed specimens disarticulate rapidly upon transport (Fig. 3.04), the abdomen breaking down readily. 'Delicate' appendages, such as antennae and mandibles, are remarkably resistant to disarticulation, and therefore give little indication of disarticulation stage.

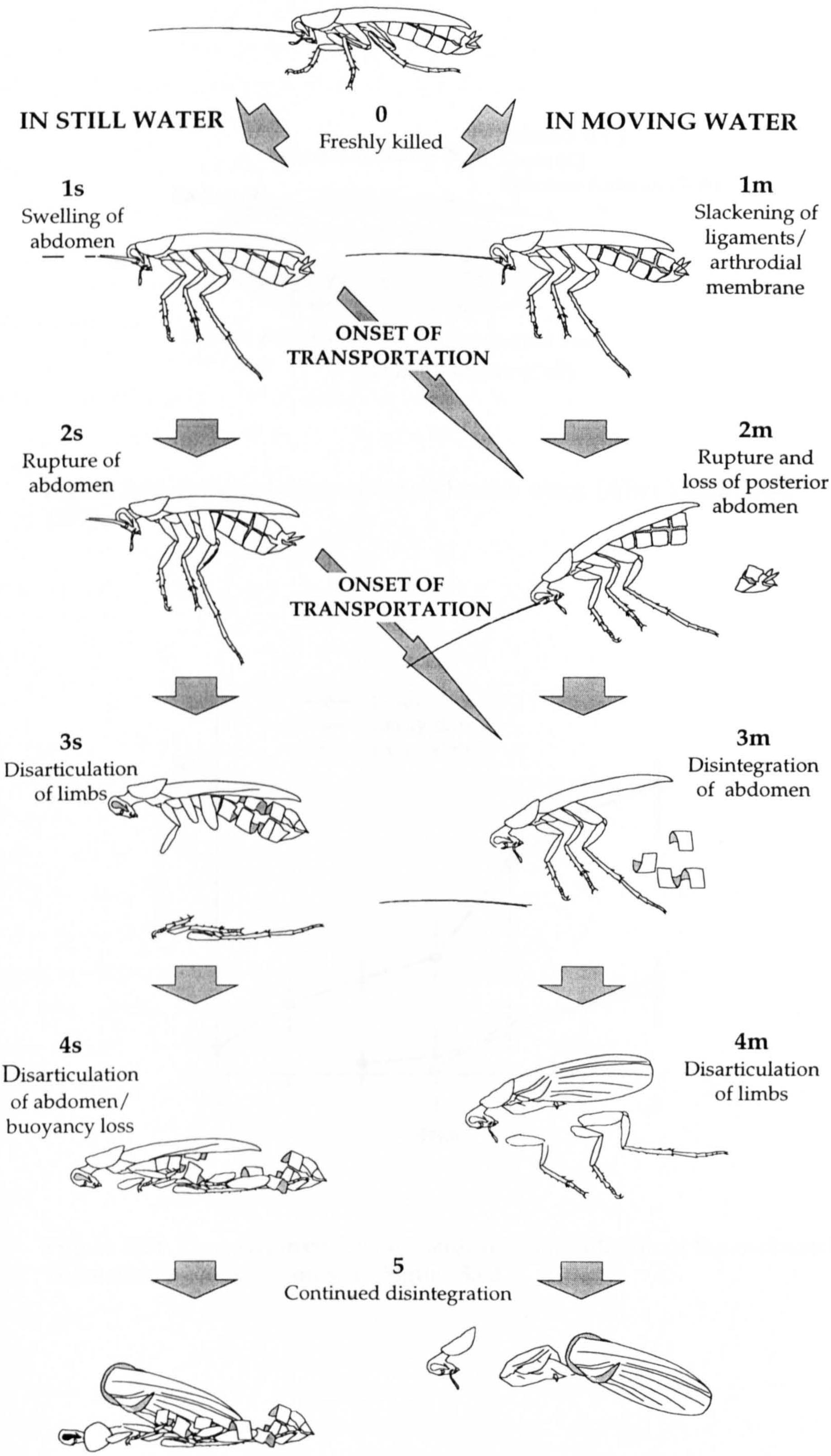


Figure 3.02 Decay and transport-induced disarticulation of the cockroach.

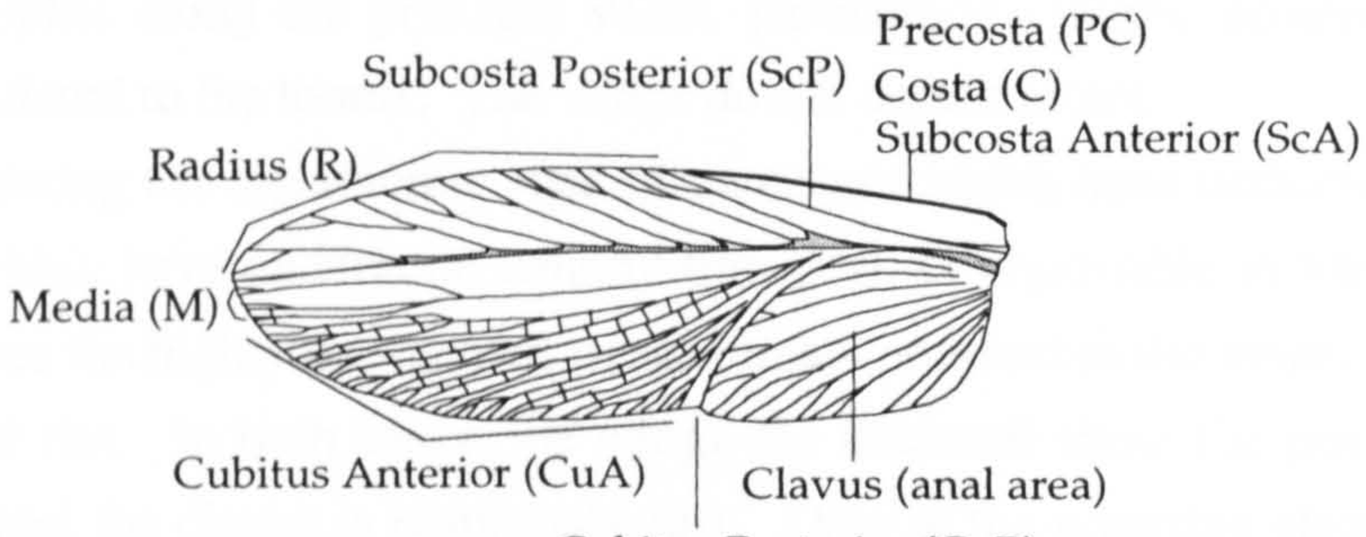


Figure 3.03 Principal veins of the cockroach wing. (After Youdeowei 1977).

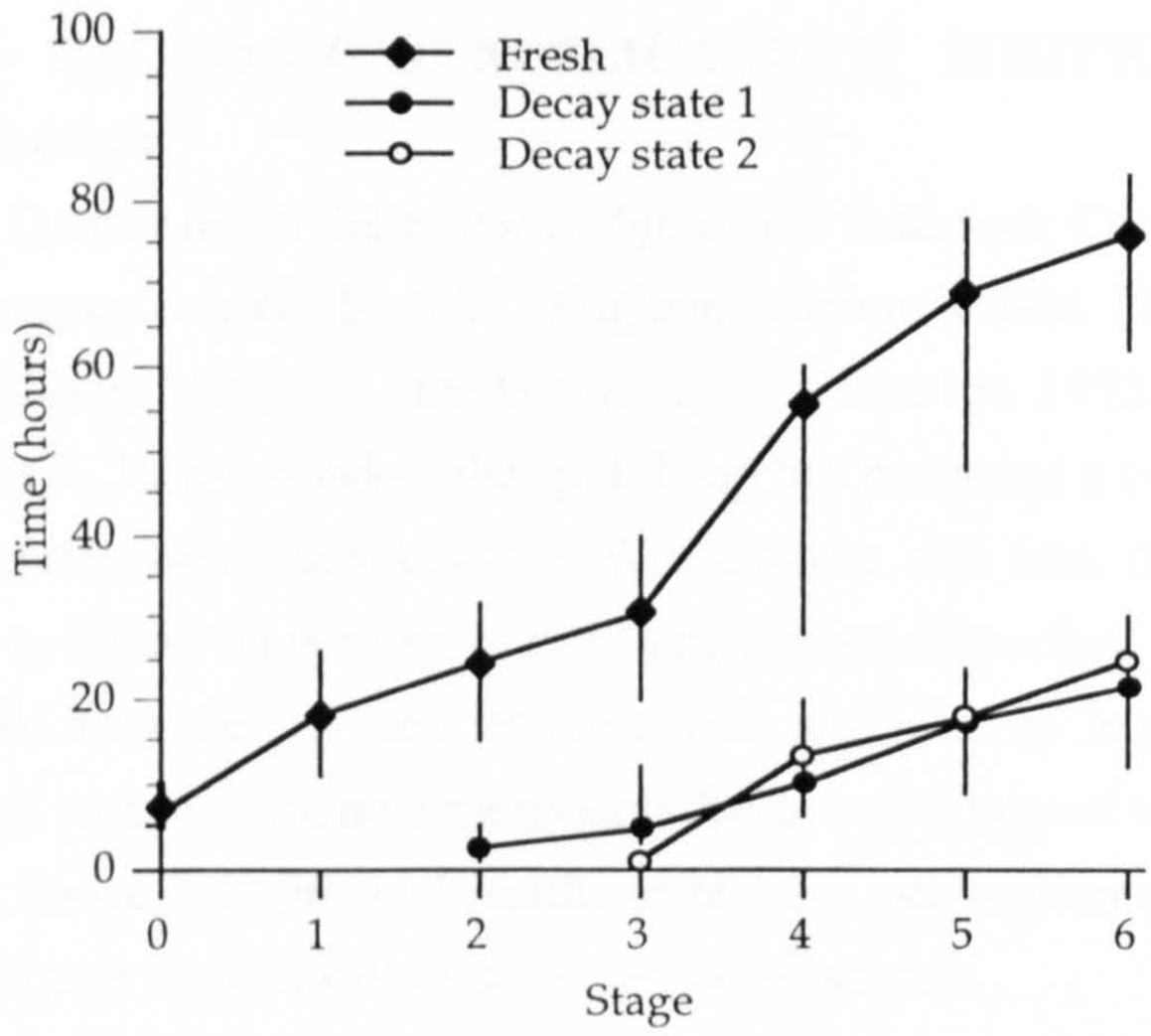


Figure 3.04 Time required for mechanical disarticulation of the cockroach. To be used in conjunction with Figure 3.02.

However, regardless of whether the carcass was decayed prior to introduction to the flume or not, the elytra remain articulated to the torso longer than any other appendage. Although the wings may begin to show evidence of deterioration, with distinctly ragged edges and splits along the principal veins, particularly cubitus posterior, they remain firmly articulated to the thorax. The wings do not detach intact.

Differentiating the taphonomic state of carcasses which have undergone decay alone, and those which have undergone lengthy transport, is impossible in hand specimen. In both instances the highly fragmented wings remain attached to the thorax for much of the experimental run. In both cases, the wings are fractured about the principal veins (see Fig. 3.03) and the clavus is commonly lost. Only at the scanning electron microscopic level is variation noted: the cuticle of decayed specimens reveals the protein vacancies noted in Chapter 2; the cuticle of carcasses which have experienced only transport-induced disarticulation reveal no such vacancies. However, differentiating between carcasses which have experienced decay alone and those whch have experienced both transport *and* decay is not possible. These experiments indicate that it is impossible to deduce the taphonomic history of the cockroach from the end products.

3.3 GEOLOGICAL APPLICATION: WRITHLINGTON

3.3.1 Introduction

Writhlington Quarry lies at the eastern edge of the Radstock Coal Basin (Westphalian D), Bristol - Somerset coalfields, S.W. England (Jarzembowski 1991b) (Fig. 3.05). A working pit for almost 150 years, the last mine was closed in 1973. Despite this, under the direction of E.A. Jarzembowksi, the spoil heap has produced a considerable collection of terrestrial invertebrates, such that the Writhlington site was declared a Geological Nature Reserve in 1985. This biota is dominated by cockroaches, primarily represented by wings. While a number of theories have been advanced to explain this taphonomic phenomenon (see section 3.1), no experiments have been initiated to investigate it. This section uses the above experimental results to test the assumption that the dominance of wings at Writhlington is the result of decay or transportation.

3.3.2 Geological Setting

The body fossils of Writhlington occur in 'roof shales' (Allen 1977), grey, finely laminated mud/siltstone, which can be subdivided into three sub-lithologies (Todd 1991). Some 90% of the fossiliferous slabs belong to sub-lithology A, a medium to dark grey, poorly to well bedded siltstone, with occasional small-scale cross-bedding (Jarzembowski 1989). The slabs are dominated by terrestrial fauna and the lycopsid *Cyperites*. The evidence suggests that this was a moderate energy environment, and it has been interpreted as an overbank deposit or a minor delta crevasse splay (Proctor 1994). *Cyperites* specimens which cross several laminae (Todd 1991) and lycopod trunks

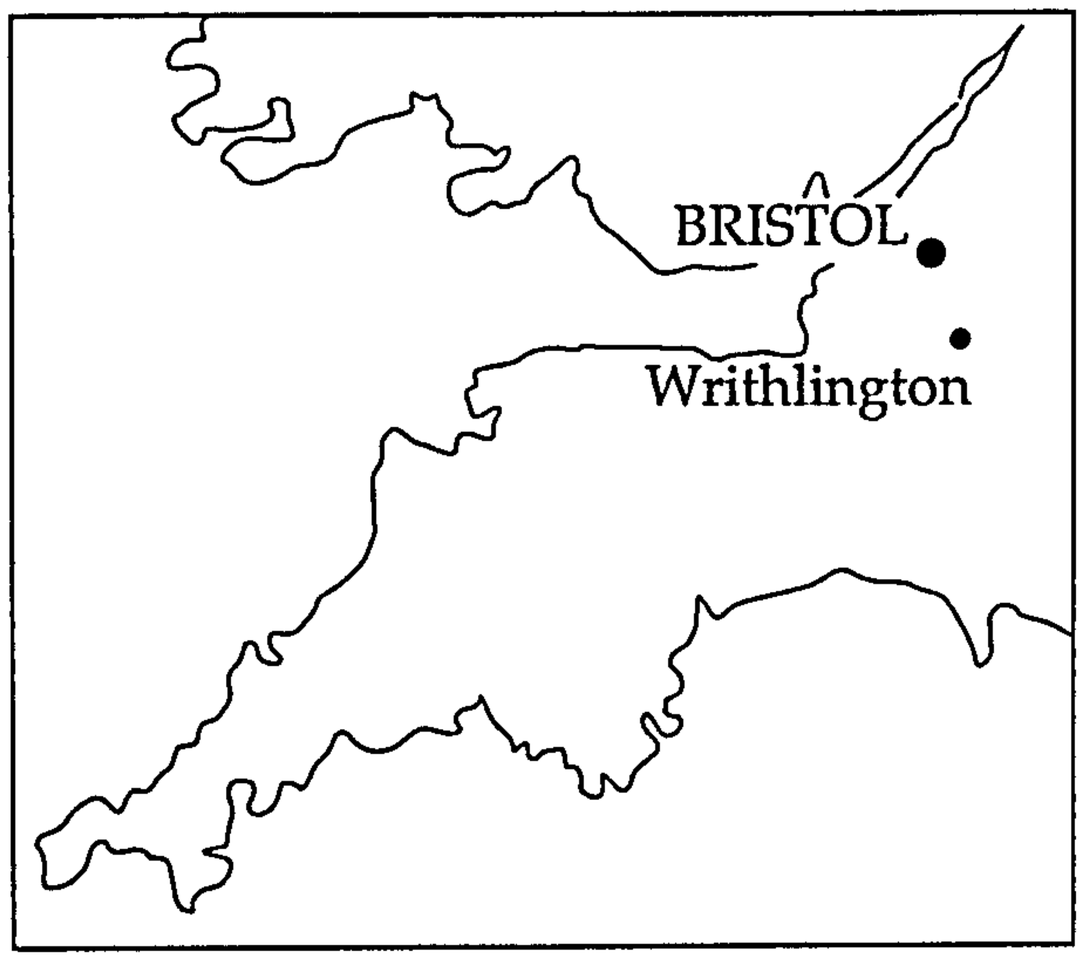


Figure 3.05 Location of Writhlington Geological Nature Reserve.

(termed 'bell moulds' by the miners) *in situ* (Proctor 1994) suggest rapid/catastrophic deposition. The vegetation and insect fauna, particularly the blattoids, suggest a tropical coal swamp, with the cockroaches living amongst leaf litter (Jarzembowski 1987, 1989, 1994), an environment comparable to that of extant blattoids (Mackerras 1970). Sub-lithology B is a medium to dark grey, regularly laminated mud/siltstone. Although body fossils are rare, trace fossils are common (Pollard and Hardy 1991). This environment has been interpreted as the margin of a muddy lake (Proctor 1994). Sub-lithology C is a light grey, non-laminated mudstone bereft of terrestrial fauna or flora, save indeterminate plant fragments (Proctor 1994), although freshwater bivalves and conchostracans are common (Jarzembowski 1989). This environment is interpreted as either a shallow, freshwater pool, or a lake margin where calm conditions predominated and there was little sediment input (Proctor 1994).

3.4.3 Biota

The fauna of Writhlington is dominated by terrestrial arthropods (Fig. 3.06), which in turn are dominated by cockroaches (~75%; Plate 3.1) (Jarzembowski 1989). Rare trace fossil evidence indicates the presence of annelids (Jarzembowski 1989) and tetrapods (Milner 1994). Fish are represented by a single scale (Bolton 1921-1922) and a small number of egg cases (Jarzembowski 1989).

The collection of cockroaches held by the Bristol City Museum (n= 581), identified to family level by E.A. Jarzembowksi of the Maidstone Museum and Art Gallery, is composed of Archimylacridae (25%), Mylacridae (10.5%), and undetermined blattoids (64.5%). They were recovered almost exclusively from sub-lithology A. No distinct taphonomic variation was noted between specimens of each sub-lithology. The blattoid specimens are dominated by wings (Fig. 3.07; Plate 3.1), and the wings by tegmina.

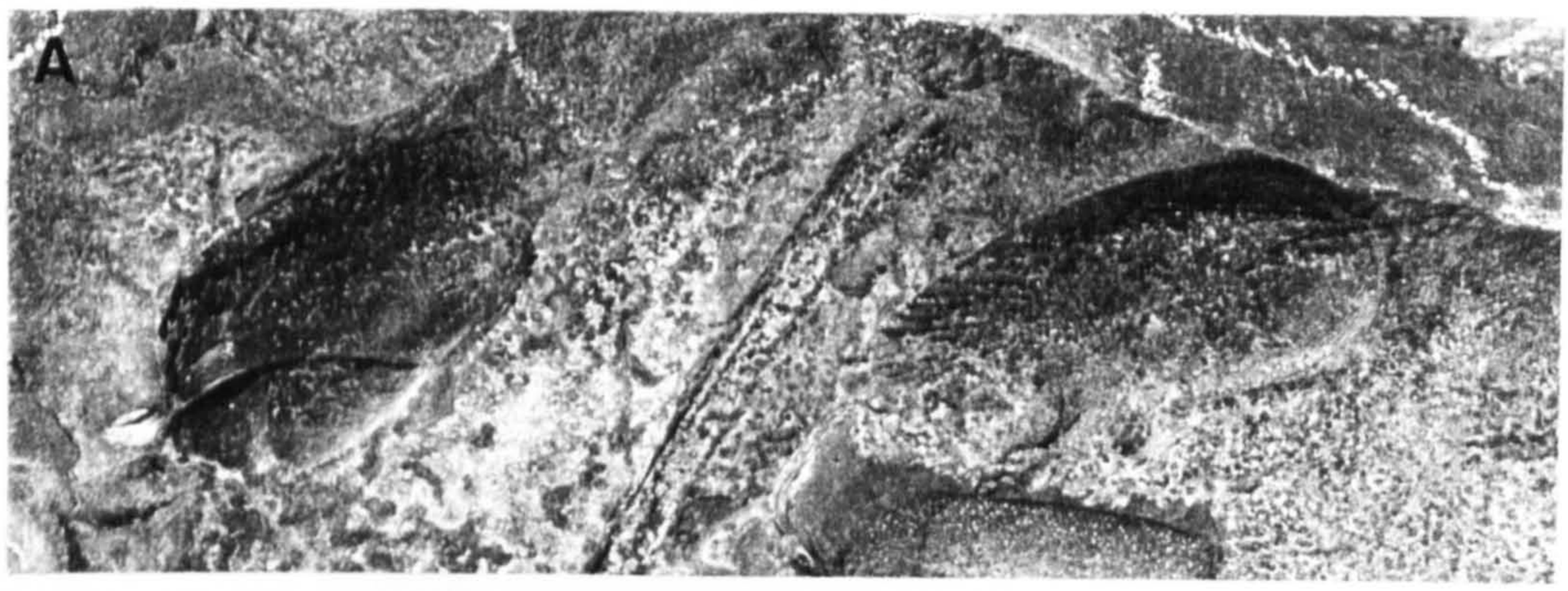
The associated flora is dominated by three groups of plants: lycopsids, the most abundant, represented predominantly by leaves, especially *Cyperites*; sphenopsids, less common; and pteridosperms, represented entirely by leaf genera (Allen 1977; Thomas and Cleal 1994; Proctor 1994).

3.3.4 Taphonomy

Cockroaches dominate the Writhlington fauna. Complete specimens are extremely rare (<1%). Wings that remain articulated, though detached from the cockroach (Plate 3.1C), or detached wings that remain in close association, account for less than 9% of the biota (Fig. 3.07; Plate 3.1A, B). The remainder of the specimens consist of isolated single wings (Plate 3.1D-F), pronota or rarely body fragments (Fig. 3.07).

Of the wings examined, only 12% were intact (Plate 3.1A-D). Fragmentary specimens account for 68% of the biota (Plate 3.1E, F). The remainder were rendered indeterminable by the fracture of the slabs and resultant loss of counterpart. Venational splitting occurs in less than 5% of intact wings

Plate 3.1 Writhlington cockroaches. A & B, Tegmen, detached but still in association. x3, x4.5 (W1033A; W487B). C, Hind wings still attached to each other. x4 (W1039A). D & F, Damaged tegmina. x3, x2 (W508A; W990). E, Intact tegmina. x2 (W402). All specimens in the collection of the Bristol City Museum and Art Gallery.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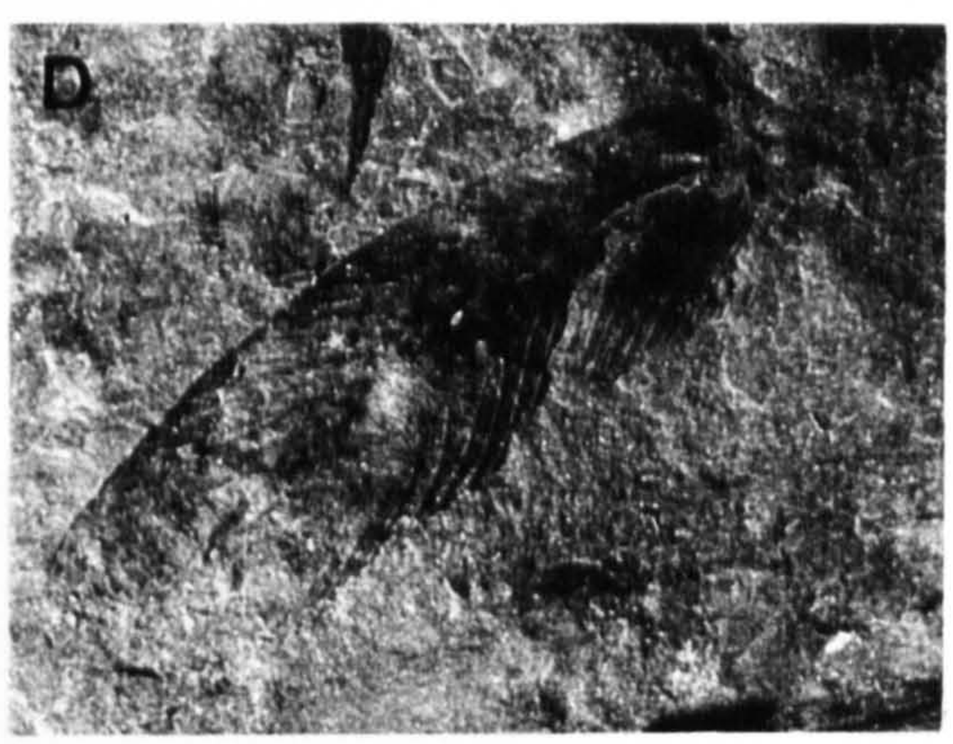
B

C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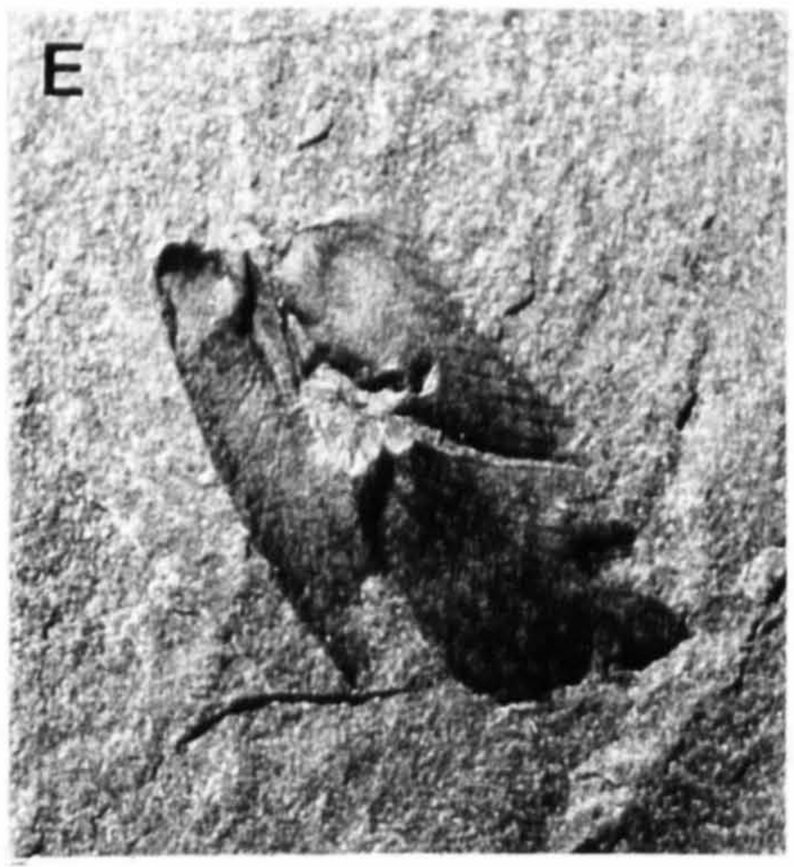
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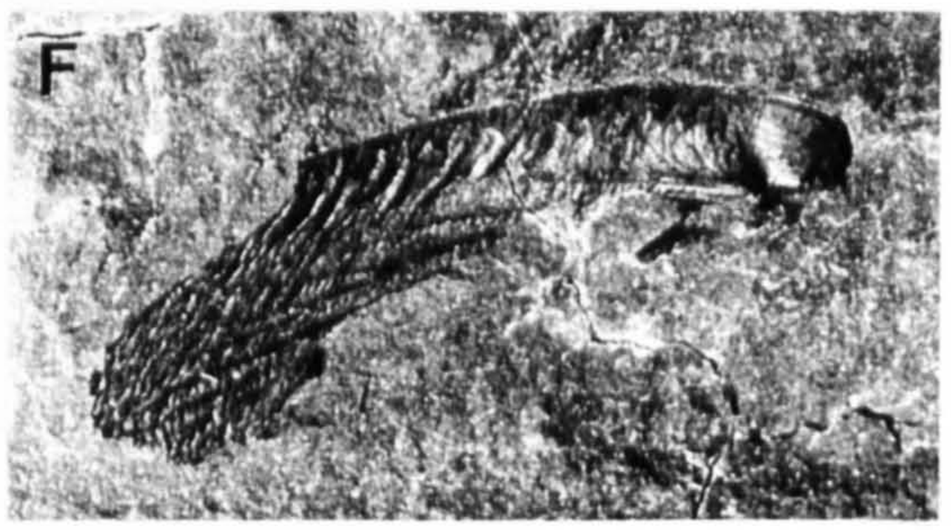
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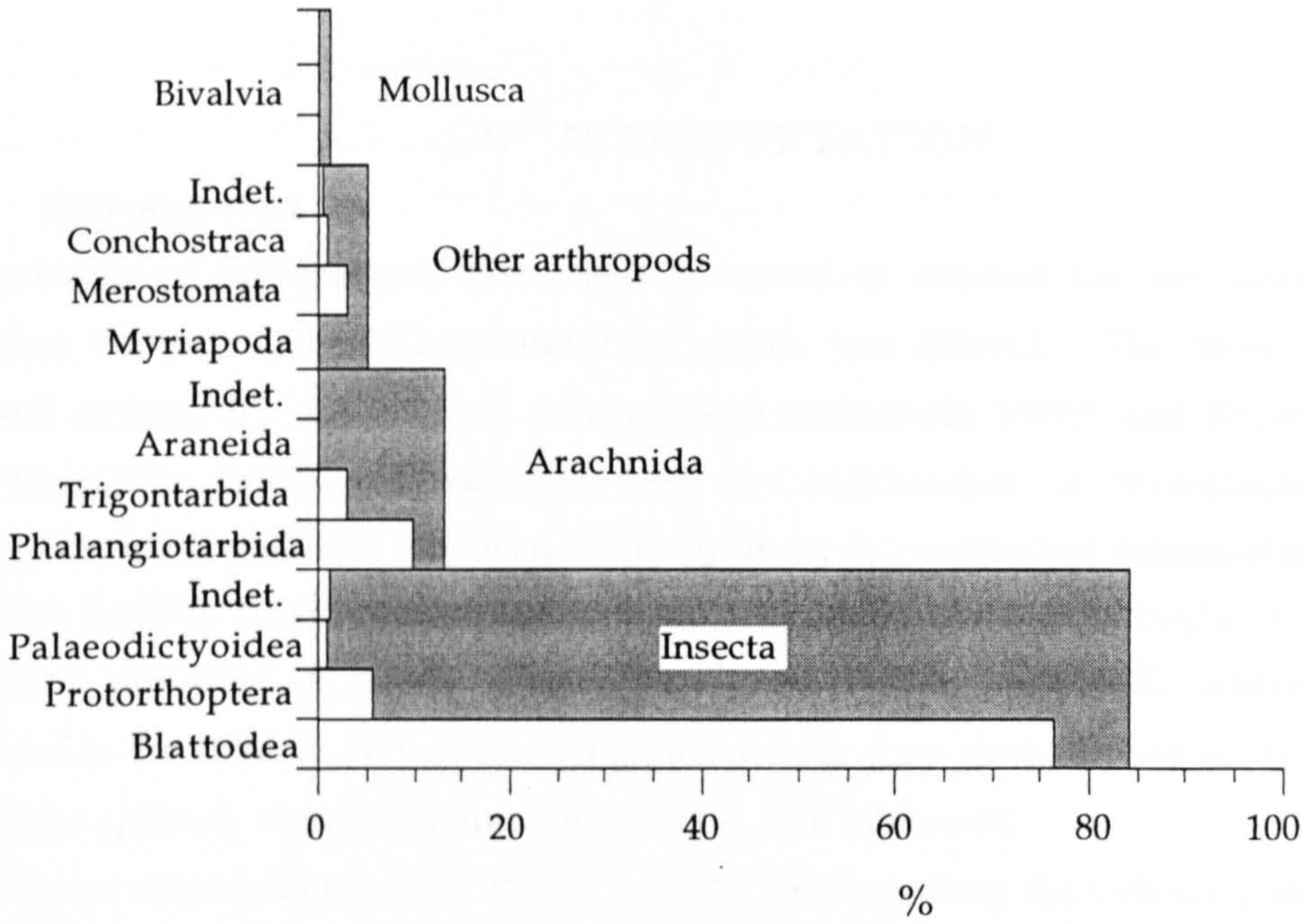


Figure 3.06 The Writhlington biota. (After Jarzembowski 1989).

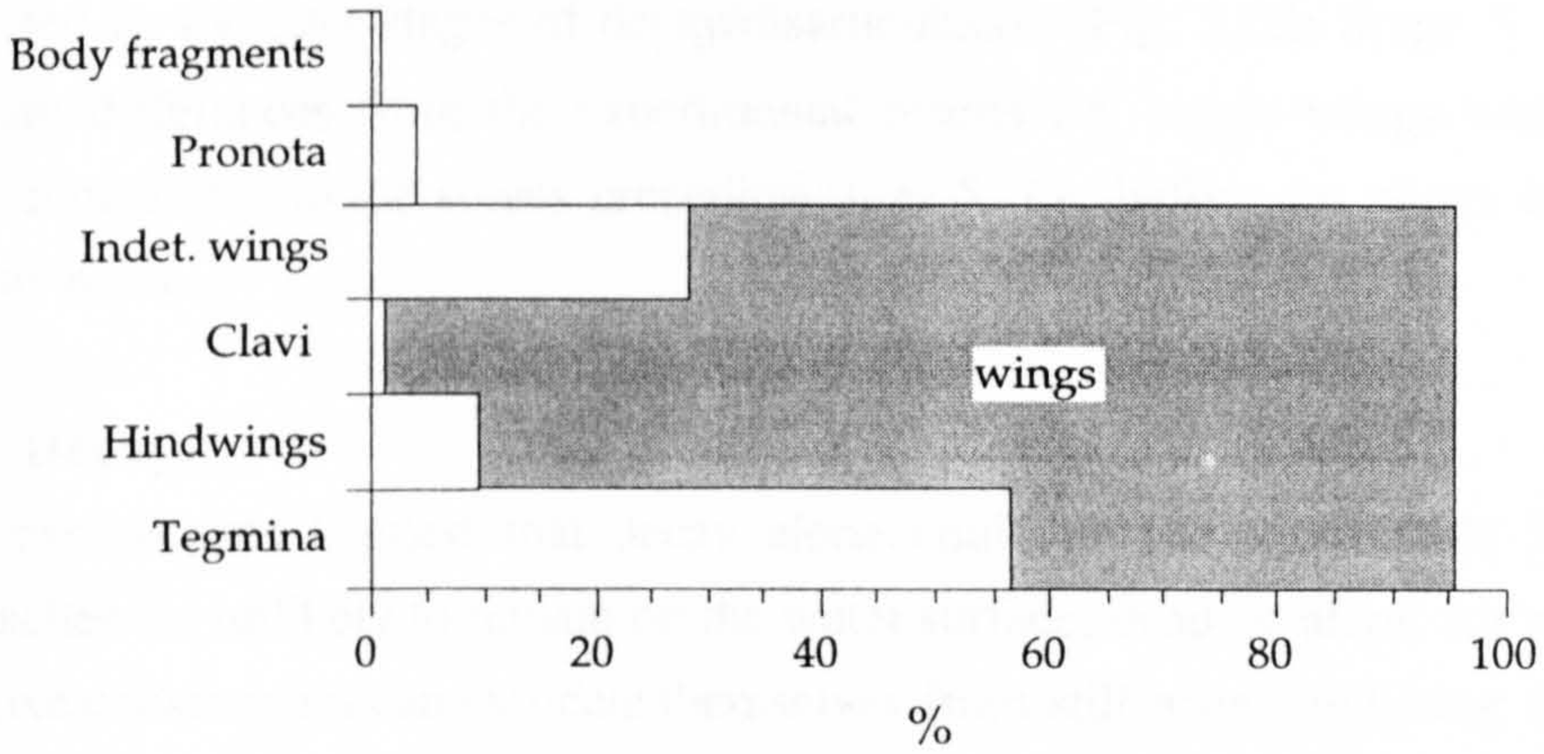


Figure 3.07 Relative proportion of cockroach wing components

Heavily sclerotized tegmen (and clavi) dominate the fauna, but a significant number of 'untanned' hind wings are reported (Fig. 3.07; Plate 3.1C). Body fragments account for less than 5% of the fauna. The preponderance of cockroach wings, to the near exclusion of all other body parts, is peculiar.

3.4. INTERPRETATION

3.4.1 Introduction

A number of explanations have been advanced to account for the dominance of cockroach wings noted in Carboniferous deposits (see above). The most commonly proposed reasons for the bias are transport (Jarzembowski 1989) and decay (Scudder 1886; Carpenter 1992). However, few of the cockroaches of Writhlington display damage consistent with that produced solely by decay or mechanical disarticulation.

During the later stages of decay (Fig. 3.02: Stage 4→), the wings begin to split along the cubitus posterior (Fig. 3.03), and the clavus is lost, *while* still relatively firmly articulated to the thorax. When the wings do detach, they generally do so as a pair, by which time splitting along the numerous veins is well advanced.

The flume experiments produced preferential splitting along the cubitus posterior vein of the tegmina (leading to the loss of the clavus), and less frequently along the subcostal vein, *before* disarticulation from the thorax (Fig. 3.03). Again, the tegmina and hind wings detach as a pair by which time wing disintegration is well advanced.

Although the fragmentary wings may represent an advanced decay/ disarticulation state, the evidence is ambiguous. While Writhlington blattoids would appear to be represented by the later stages of decay/disarticulation (Fig. 3.02; Stage 5→), there are significant differences from the experimental results *i.e.* single wings which are more directly comparable to the stages preceding stage 5, *i.e.* before the wings began to split along the veins.

3.4.2 Decay

The experiments suggest that decay alone could not be responsible for the bias. Cockroaches are unlikely to remain on the water surface, dead or alive, for any length of time. Live cockroaches can extricate themselves from still water, reducing the likelihood of accidental drowning. Carcasses are unlikely to remain on the surface for the significant period that proceeds carcass disintegration and loss of buoyancy without attracting the attention of scavengers. If by some means an intact carcass broke the surface tension and descended to the bottom, the elements would remain in close association (see Lutz 1990). However, disarticulated components of the same carcass are rarely found on the same bedding plane. A decaying carcass trapped at the thermocline of a stratified lake could disintegrate undisturbed by scavengers and scatter its components over a wide area with the turnover of the waters. However, the ratio of wings to other

recovered body fragments should remain consistent. This is not the case. Also, stratification requires a water body of considerable depth, which is at variance with the current environmental reconstruction (see Proctor 1994).

3.4.3 Transport

The experiments also suggest that transport acting alone could not produce the noted damage to the wings. The dominant cockroach-bearing lithology of Writhlington is indicative of moderate energy and is interpreted as an overbank deposit or minor deltaic crevasse splay, suggesting minimal transport. This is in broad agreement with Proctor's (1994) study of the plant fossils, in which he concluded that the floral assemblages were too homogenous for transportation to have acted as a significant taphonomic filter, since this would have dispersed the various floral components into different assemblages. Jarzembowski (1989) and Todd (1991) state that the presence of well preserved articulated arthropods (though rare) implied minimal transport. However, their reasoning is incorrect; preservation of delicate appendages or complete specimens, as shown by the experiments is not in itself evidence of limited transport (see Allison 1986).

3.4.4 Alternative explanations

The experimental results therefore beg the question, what produces isolated wings and wing fragments? The suggestion that the dominance of wings is attributable to collecting bias (see Bolton 1921; North 1931) has already been refuted by Jarzembowski (1987). North (1931) and Todd (1991) have suggested that predation may play a more important role than has hitherto been suggested. Possible Writhlington predators include chelicerates (Dunlop 1994) and protorthopterans (Bolton 1921; Jarzembowski 1989) known from body fossils, and xiphosurans (Anderson 1994) and reptiles (Milner 1994) known from traces.

Direct testing of the results of predation is hampered by the extinction of a number of the leading predator candidates. Reptiles tend to be indiscriminate feeders, eating the insect whole (N. Alexander, *pers. comm.*). Although recognizable fragmentary remains may be extracted from the faecal pellets, they are not comparable to the Writhlington material. Xiphosura would also have been indiscriminate feeders (L.I. Anderson, *pers. comm.*).

An analogue of the phalgotarbids/trigonotarbids is the modern spider (order Araneae). Feeding behaviour differs markedly among the various spider families and depends on whether cheliceral teeth are present (Foelix 1982). Spiders which lack such teeth inflict only small wounds on their prey. Digestive fluid is pumped in and out through this hole and the dissolving tissue is gradually sucked out. After the meal, the prey remains an empty sac that may appear externally unharmed. This empty sac quickly becomes brittle, and the wings readily detach. Spiders with cheliceral teeth, such as the 'tarantula' mash up their prey rendering the carcass unidentifiable (see Gerhardt and Kaestner 1938).

However, the wings are often severed during the feeding struggle (N. Alexander, *pers. comm.*). In both instances the wings and body fragments become become part of the leaf litter where decay and scavenging of the cuticle will continue. The heavily sclerotized tegmen and wings are more likely to survive this process (see Okafer 1966b; Seastedt and Tate 1981; Seastedt and Crossley 1984). Ultimately the leaf litter and wings may be mobilized and transported by running water. A deluge of the Writhlington delta area (as suggested by the *in situ* tree stumps) could transport this material, and deposit it rapidly.

3.5 IMPLICATIONS

The above experiments provide both qualitative and quantitative data on the decay and disarticulation of cockroaches in a fluvial environment. Examination of the cockroach fossils of Writhlington, south-west England, in light of such findings, revealed that neither decay nor transport acting alone, or together, are likely to have have produced the observed cockroach specimens of Writhlington. The most likely explanation would apear to be predation of the cockroach with the spider and its extinct relatives the most likely candidate.

There are a many Carboniferous deposits from which cockroaches have been recovered in significant numbers (see Chapter 1, Table 1.2). However a hurdle common to the study of their taphonomy is the selectivity of the various collections. Often only the more complete, or impressive specimens, were recovered from a site, with the less complete or damaged discarded. This is a particular problem in those collections established prior to the advent of taphonomic study (*ca.* 1970). Only a limited number of collections exist where all specimens regardless of condition or intactness are recovered. The Mazon Creek collection of the Field Museum of Natural History (Chicago) is one such collection (see Chapter 4). Application of the above experimental results to those specimens may prove instructive to the understanding of decay and fluvial transport in the Mazon rivers. However, the other collections are unsuited to taphonomic study. It is therefore imperative that the recovery of specimens from a single deposit in the future include all the material uncovered.

CHAPTER 4

MAZON CREEK

4.1 INTRODUCTION

The earliest true insects are recorded from the massive coal swamps of the Late Carboniferous (Carpenter 1992; see Chapter 1.5.2 for a review). Since strata of this age are the most extensively mined of sedimentary rocks, much is known of the biota and its palaeoecology. Insects, generally consisting only of wings, are amongst the most common components of the fauna (see Chapter 3). Articulated, three-dimensional specimens are rare, and are predominantly recovered from the small, ferruginous concretions found in certain deltaic cyclothemic settings, generally in the grey shale above coal horizons (Baird *et al.* 1985a).

Fossil-bearing concretions occur in significant numbers in only a few areas: Missouri and Oklahoma, U.S.A. (Baird *et al.* 1985a); Montceau-les-Mines, France (Heyler 1980); the Coal Measures at Rochdale (Woodward 1907, 1908, 1911) and Lancaster (Bolton 1905, 1921-22, 1934), U.K.; and the fresh to brackish water turbidites of Bude, U.K. (White 1939; Burne 1969). However, the best documented concretions are those of the celebrated Mazon Creek region (Upper Carboniferous: Westphalian D) of northeastern Illinois, U.S.A. (Johnson and Richardson 1966; Baird *et al.* 1985a, b, 1986) (Fig. 4.01).

The Mazon Creek biota includes the most important assemblage of soft-bodied invertebrate fossils known from the late Palaeozoic (Baird *et al.* 1985b; Baird 1992), as well as one of the most diverse terrestrial floral assemblages (Horowitz 1979). Its proximity to Chicago has ensured that the area has been scoured by fossil hunters, both amateur and professional. A large census collection is housed in the Field Museum of Natural History, Chicago. Amassed from over 360 locations and including every fossil found at each locality, regardless of state of preservation, the collection presently includes over 20,000 specimens, and is probably one of the most complete palaeoecological collections in the world (P.R. Crane, *pers. comm.*).

4.1.1 Aims and scope of work

Despite considerable research on the taxonomy of the Mazon Creek biota and its palaeoecology (*e.g.* Nitecki 1979, and references therein), little taphonomic work has been conducted. To date, studies have generally focused upon concretion growth with little regard for the fossil within. Indeed, almost all of the isotopic/geochemical studies have been made on material from which significant macrofossils are absent, making it

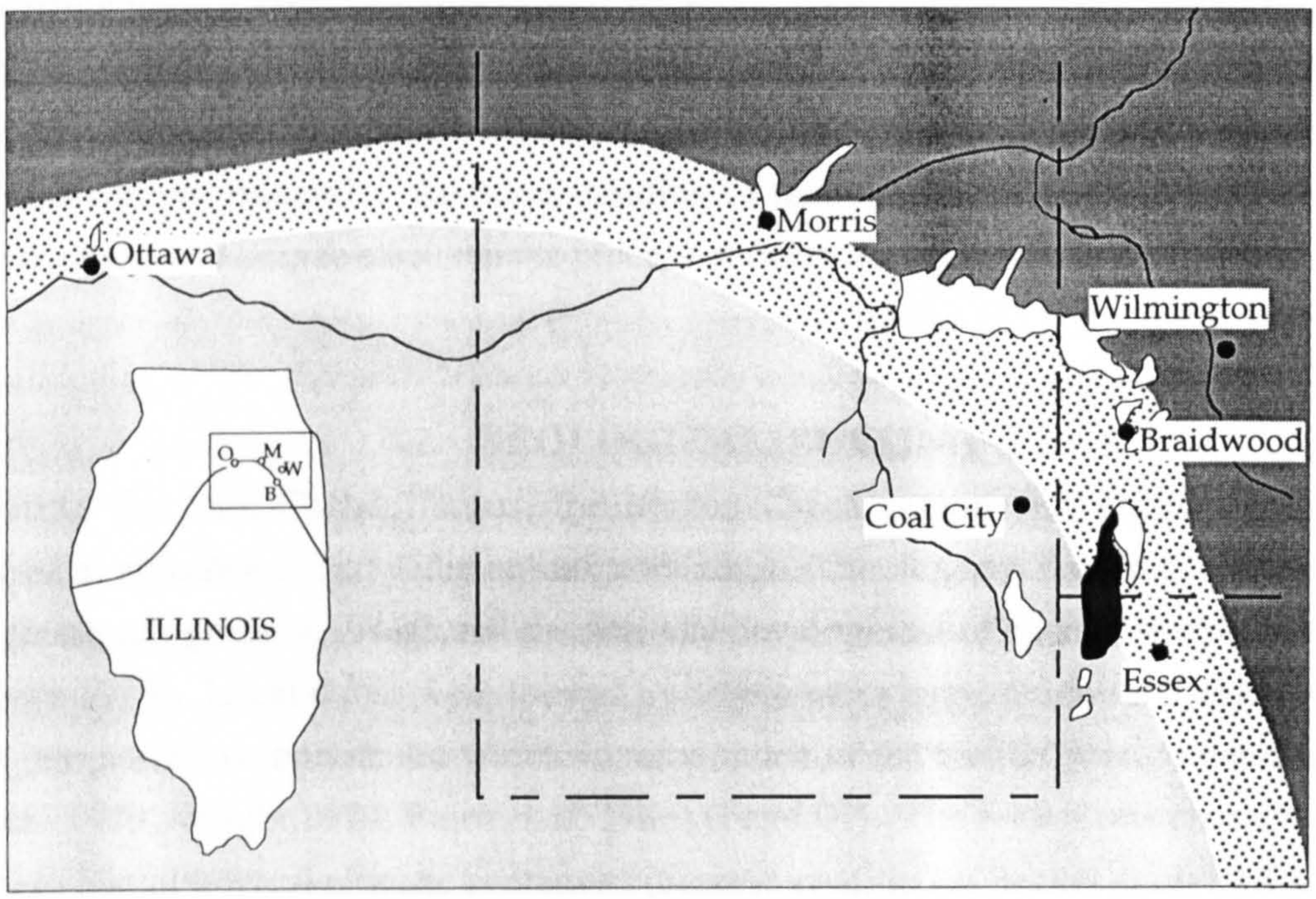


Figure 4.01 Mazon Creek region of northern Illinois showing the location of the principle strip and underground mines. Stippling represents palaeoenvironmental reconstruction of Richardson and Richardson (1971). **Inset** Map of Illinois showing location of Mazon Creek region. Line represents the margin of fully marine fauna. Box length = 90km.

difficult to compare the fossiliferous and non-fossiliferous end products of concretion growth (Canfield and Raiswell 1991b). This chapter attempts to remedy this deficiency by focusing upon a representative sample of the insect specimens of the Field Museum. Many of the Mazon Creek fossils are preserved as no more than impressions often dissected by septaria (Baird *et al.* 1985b). However, some of the insects are replicated by a diverse suite of minerals. An understanding of their chemistry and the processes of mineralization will help to elucidate the process of concretion formation.

4.2 GEOLOGICAL SETTING

During the Late Carboniferous, the Mazon Creek region was characterized by differential subsidence and sediment accumulation. The deposits record cyclic marine transgression/regression events and the periodic development of extensive coal swamps (Shabica 1979). Local deltas were formed by one or more large, sluggish rivers flowing south into a shallow epeiric sea which covered much of the area of present day Illinois (Nitecki 1979; Wright 1979; Baird *et al.* 1986) (Fig 4.01). The region was characterised by dry to humid tropical climatic conditions (Scotese *et al.* 1979; Heckel *et al.* 1980).

The Mazon Creek fossils are recovered from the lowest part of the Francis Creek Shale Member, Carbondale Formation (Westphalian D: Pfefferkorn *et al.* 1971) (Fig. 4.02). This regionally discontinuous unit consists of lenticular wedges of terrigenous sediment which were deposited in a cyclothemic deltaic setting upon the Colchester Coal Member during a broad phase of delta progradation (Wright 1965; Shabica 1979; Baird *et al.* 1985a). The sediments vary from laminar grey shales (interpreted as interdistributary bay deposits: Shabica 1979) which contain the fossil-bearing concretions, to thick, cross-bedded sandstones with erosional bases (interpreted as crevasse splay deposits: Johnson and Richardson 1966; Nitecki 1979).

4.3 BIOTA

The concretions reveal an abundant and varied flora and a fauna including both biomineralized skeletons and soft-bodied animals. Two major habitats are represented: the terrestrial, swampy, forested lowland of the subaerial delta (Braidwood fauna) and the shallow waters of the marine margin (Essex fauna) (Johnson and Richardson 1966; Baird *et al.* 1985a, b). The Braidwood association can be further subdivided on the basis of its floral and faunal content into terrestrial (insects, arachnids and tetrapods) and aquatic (crustaceans, xiphosurans, merostomes, clams, ostracodes, fish and amphibians) realms (Schram 1979). Over 350 named species of land plants have been reported (Horowitz 1979). The 206 named species of land arthropod are dominated by insects (140), with millipedes, centipedes, spiders and their allies, and scorpions completing the group (Fisher 1979). Although diverse, insects are relatively rare and comprise only 4.8% of

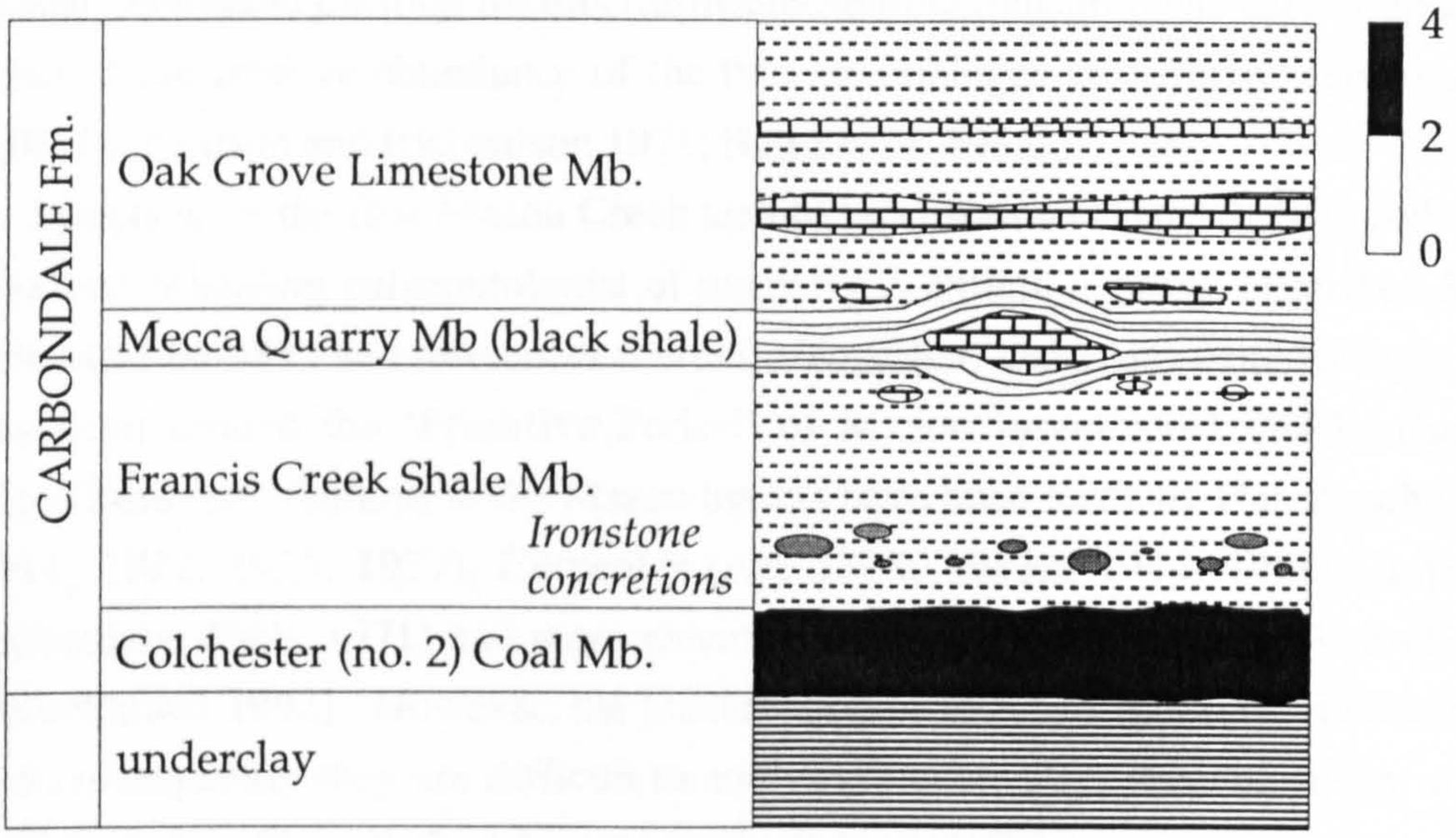


Figure 4.02 Stratigraphic setting of the Francis Creek Shale Mb, western Illinois, where it thins (3-5m). (After Baird 1979).

the total individuals recovered. The Braidwood association is thought to have been derived from the catchment area of a source river. The marine Essex assemblage, thought to have been swept in by tidal action, includes a diverse range of cnidarians, worms, molluscs, holothurians, shrimps and fish (Fisher 1979). An approximate palaeogeographic position for this freshwater/marine transition has been proposed on the basis of the relative abundance of the two assemblages at different census sites (Fig. 4.01: Richardson and Richardson 1971; Baird *et al.* 1985a).

Insects were the first Mazon Creek taxa to be described (Dana 1864). Subsequently, Scudder, a leading palaeontologist of the early twentieth century, described 36 species (see Scudder 1885 and references therein). Together, Dana and Scudder represent what has been termed the 'Primitive Period' of Mazon insect work (Richardson 1953). Significant contributions to the Mazon insects have been made by Handlirsch (*e.g.* 1906, 1911, 1922, 1925, 1937), Carpenter (*e.g.* 1938, 1943b, 1944, 1964; Carpenter and Richardson 1968, 1971) and more recently Kukalová-Peck (1987; Kukalová-Peck and Brauckmann 1992). However, the preservation of insects is poor, or at best indifferent and consequently they are difficult to analyse faunistically, particularly by anyone not intimately familiar with the relevant groups (Schram 1979).

4.4 GENERAL TAPHONOMY

4.4.1 Concretion occurrence

The vast majority of the fossil concretions have been recovered from the bings created by the opencast mining of the economically important Colchester Coal (Richardson 1956) (Fig. 4.02). Fossils on bedding planes, although noted, are rarely recovered due to the rapid disintegration of the shales on the spoil heaps. Only locally indurated bedding planes preserve specimens for sufficient time to allow collection (Richardson 1956).

The siderite concretions are commonly smooth and symmetrical, although some are irregular and may be formed of two adnate concretions (Richardson 1956). They range in size from a few centimetres to almost half a metre; the larger ones are invariably septaria without fossils. The fact that bedding planes continue through randomly distributed *in situ* concretions indicates that the concretions are autochthonous (Richardson 1956). Concretions split along planes of weakness, generally the fossil, and many have already broken in the field due to the freeze-thaw action of the harsh Illinois winter. There is no correlation between the size of the fossil and the size of the concretion. Not all concretions are fossiliferous, and barren concretions make up the largest component of some samples.

4.4.2 Preservational categories

Four broad categories of concretionary fossil are recognized: plants, shelly animals, soft-bodied organisms, and sclerotized organisms (Allison and Pye 1994). Plant fossils

are preserved as carbonaceous permineralizations, with associated sulphide minerals such as pyrite and galena. Although robust cones and fruit are strongly three-dimensional and retain some internal structure, more fragile organs such as leaves preserve no internal detail (Schopf 1979). Plant fossils are also recovered from the host sediment, where they are preserved only as impressions (Richardson 1956). The skeletal carbonate of shelly animals such as molluscs and brachiopods has been removed and the cavities commonly filled with quartz, calcite, galena, pyrite or sphalerite, which can replicate small-scale growth laminae and ribbing (Schopf 1979). Soft-bodied organisms include medusoids (Foster 1979a), polychaete worms (Thompson and Johnson 1977), holothurians, hydroids (Schram and Nitecki 1975) and the enigmatic Tullymonster (Foster 1979b). Medusoids and the Tullymonster are preserved as film-like impressions with a degree of surface topography (Allison and Pye 1994). Polychaetes and holothurians preserve both dorsal and ventral integument, separated by a discernible infill (Allison and Pye 1994). Polychaetes are most commonly preserved as external moulds with dickite, galena or pyrite infills, while holothurians are often coated with haematite. Heavily sclerotized organisms such as xiphosurans, some larger eumalacostracans, and some insects are entirely three-dimensional (Anderson 1994; Kukalová-Peck and Brauckmann 1992; Allison and Pye 1994). While the xiphosurans and eumalacostracans may appear to preserve cuticle, it is in fact a fine layer of iron minerals (Allison 1988d). While most of the insects are composed only of iron minerals, some are composed of a varied suite of minerals.

4.5 FOSSIL PRESERVATION

4.5.1 Introduction

4.5.1.1 Conditions favouring concretion growth. The fresh/ brackish water deltaic environment of the Mazon Creek (Baird *et al.* 1985a, 1986) provides ideal conditions for the instigation and growth of early diagenetic carbonate concretions (see Allison 1991; Canfield and Raiswell 1991b). The high organic input of the 'Mazon River(s)' (comparable in scale to that of the Mississippi) and its subsequent decay are of primary importance to the formation of carbonate concretions. It is generally recognized that carbonate supersaturation is brought about by the alkalinity generated from the microbial decay of organic matter (Postma 1981; Coleman and Raiswell 1981; Canfield and Raiswell 1991b). In the presence of oxygen, microbial respiration produces CO_2 which, as carbonic acid in pore water, promotes carbonate dissolution. However, in the absence of oxygen, the sediment microbiota utilize a series of alternative oxidants in the respiration process, such as manganese, nitrite, iron or sulphide (see Allison 1991), the common denominator of which is the production of the carbonate ion (Canfield and Raiswell 1991b). If this ion reacts with a suitable cation, such as calcium, iron, magnesium or manganese, then a carbonate mineral may form. The mineral formed is

dependent upon the dominant decay pathway at the site of deposition. In the marine environment, water is normally saturated with respect to calcium (while the concentration of iron is low), resulting in the precipitation of $CaCO_3$. However, in river-dominated estuaries and deltaic settings, there is usually an abundant supply of iron, which favours siderite stability (Curtis and Spears 1968; Ho and Coleman 1969; Berner 1971; Woodland and Stenstrom 1979; Canfield and Raiswell 1991).

Concretion instigation is therefore controlled by three primary factors: anoxicity, Eh and pH, which in turn are directly controlled by the input of organic detritus to the sedimentary sequence and its subsequent anaerobic decay (Berner 1981; Canfield and Raiswell 1991b). It has been argued that concretion growth is not solely controlled by the alkalinity generated by the microbial decay of soft-tissue (see Zangerl *et al.* 1969; Dickinson and Barber 1976; Raiswell 1976). Current understanding of the disparate available evidence suggests that where concretions contain readily metabolizable organic matter, its rapid decay may locally enhance supersaturation to the point where cementation can occur around, and in the vicinity of, the soft-bodied material (Canfield and Raiswell 1991b).

4.5.1.2 Timing of concretion growth. Concretion growth must begin before decay destroys its organic nucleus. The fact that the concretions of the Mazon Creek preserve jellyfish, yolk sacs on larval fish, colour markings on bivalves and insects, setae on worms, and radulae of both chitons and cephalopods indicates relatively *rapid* burial of at least these organisms followed by encapsulation within early diagenetic concretions (Baird *et al.* 1985a). Preserved porosities and textural evidence confirm an early diagenesis. Since concretionary siderite precipitates predominantly within sediment pore-spaces, the volume of concretion-forming mineral is equal to sediment porosity at the time of carbonate precipitation (Lippmann 1955; Raiswell 1976). In carbonate concretions, the original porosity is approximately equivalent to the acid soluble fraction of the concretion. Using this method, the internal porosity of some Mazon concretions has been shown to be as high as 80-90% at the centre, *i.e.* indicative of the upper 10m of sediment, while porosity at the rim can be as low as 50%, suggesting concretion growth continues as the concretion is compacted with depth (Raiswell 1976; Allison and Pye 1994).

The timing of growth can also be constrained by comparison of the Carboniferous sideritic concretions with modern examples. However, finding such an analogue has proved problematic. The Holocene marshes of North Norfolk (Pye 1981, 1984, 1992; Pye *et al.* 1990; Allison and Pye 1994), and the delta of the Mississippi (Coleman 1966; Coleman and Ho 1969; Tye and Kosters 1986; Moore *et al.* 1992) are thought to be the nearest analogues.

The abundant fossiliferous concretions of the Norfolk marshes are composed of siderite, calcite and iron monosulphides (Pye 1984; Allison and Pye 1994). Their rate of

growth can be determined since some concretions have concreted around munition fragments dating from the Second World World (mollusc shells and wood are more common nuclei). Mineralisation began with the infilling of primary skeletal voids, and continued with the replacement of the shell itself, preserving laminations of the shell but not crystal morphology (Allison and Pye 1994). Stable isotope analysis (C and O) indicates that the shell itself is the source of the carbonate, with shells of aragonite more highly sideritized than those of calcite. Plant material may also be preserved: cell walls may be coated or replaced by siderite, and the cells infilled by siderite or iron monosulphide; roots and stems can be infilled with siderite, iron monosulphide or calcite. Experiments have thus far succeeded only in precipitating siderite around aragonitic nuclei (Allison and Pye 1994). No precipitation has been produced about non-mineralised nuclei.

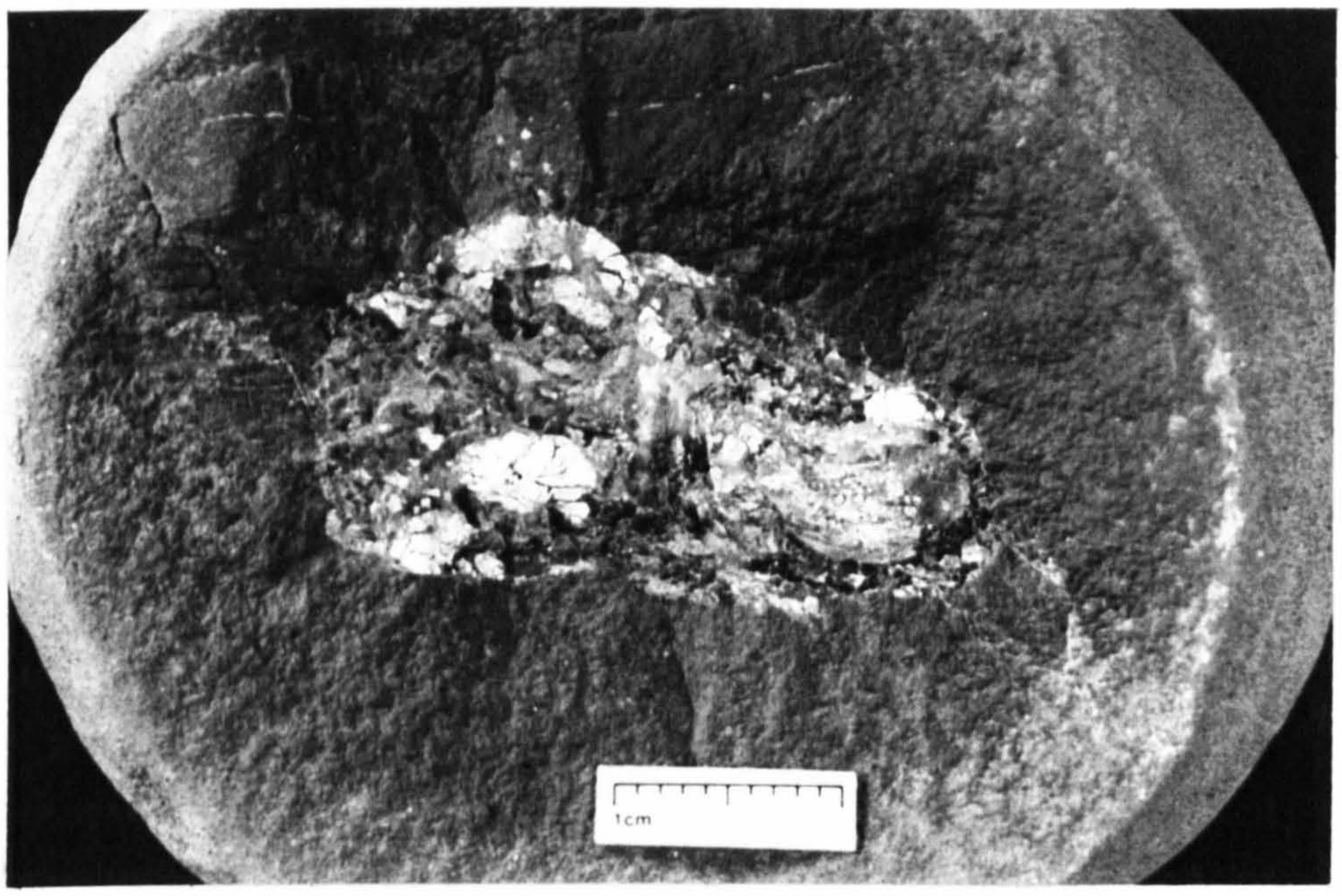
A number of concretions have been found in cores from the Terrebonne Bay region of the Mississippi River delta (Moore *et al.* 1992). The area is experiencing rapid subsidence and what was previously freshwater marsh is now occupied by brackish and salt-water marsh grass. The sediments have been deposited in the last 1500 years (^{14}C dating: Roberts 1986). The concretions (1-2cm in diameter) often preserve rootlets and burrows, but no trace of relict shell material or detrital carbonate fragments have been found within. Initial pore water was considered to be fresh, favouring the precipitation siderite. No organic nuclei, about which the concretion grows, is mentioned. Following marine inundation, calcitic deposition is favoured and precipitates about the sideritic core. Where the pore waters are more saline, calcite may comprise up to 50% of the peripheral zone of the concretion.

4.5.2 Analysis of concretions

4.5.2.1 Materials and method. The arthropod collection of the Field Museum of Natural History, Chicago was studied during a short visit in the autumn of 1995. The insects are diagnostic of the Braidwood fauna. Most retain a degree of three-dimensionality (see Kukalová-Peck and Brauckmann 1992: Fig. 1, 2, 5 and 11). Wings are most common. Most specimens are preserved as impressions within the host sediment. A limited number of specimens are infilled with a varied suite of minerals discernible to the naked eye (see Plate 4.1A, B). A representative sample of 11 specimens (including members of Protorthoptera and Blattodea as well as several indeterminate specimens) was borrowed, and permission secured for analysis. Three of the specimens include both part and counterpart. Specimens with a mineral infill (n=6) and those without (n=5) were selected for comparison.

Permission was granted for non-destructive analyses (electron microprobe, scanning electron microscopy, elemental mapping). In addition, permission was given to remove mineralised fragments from a single cockroach specimen (FMNH PE32054: Plate 4.1A) for X-ray diffractive analysis.

Plate 4.1A Indeterminate protorthopteran (FMNH PE32054). A, Specimen from which material was extracted for XRD analysis. B, *Camera lucida* sketch of fossil highlighting mineral variation. Specimen recovered from Pit 11, Peabody Coal Company, Illinois. [Field Museum of Natural History (Chicago)].



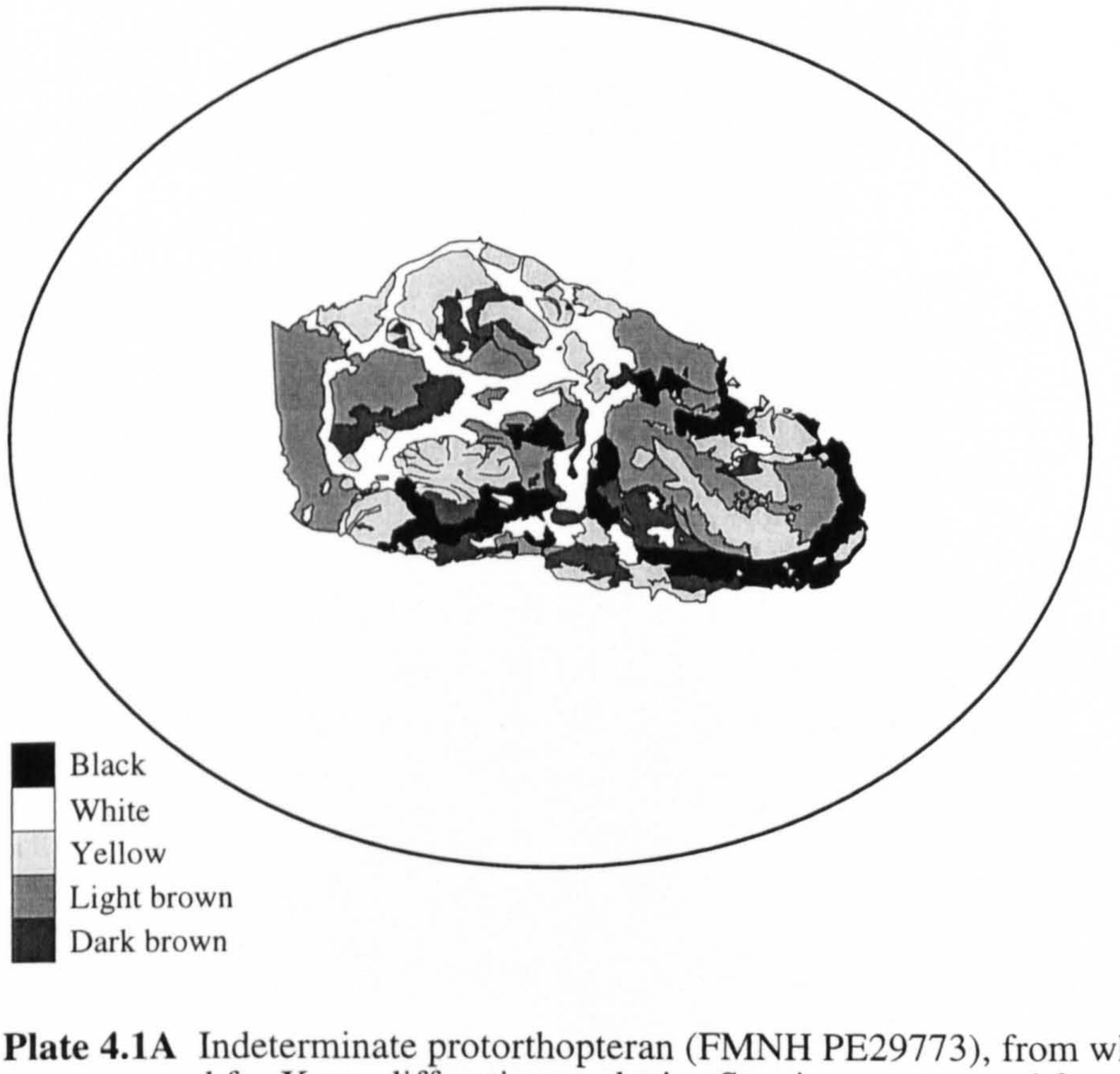
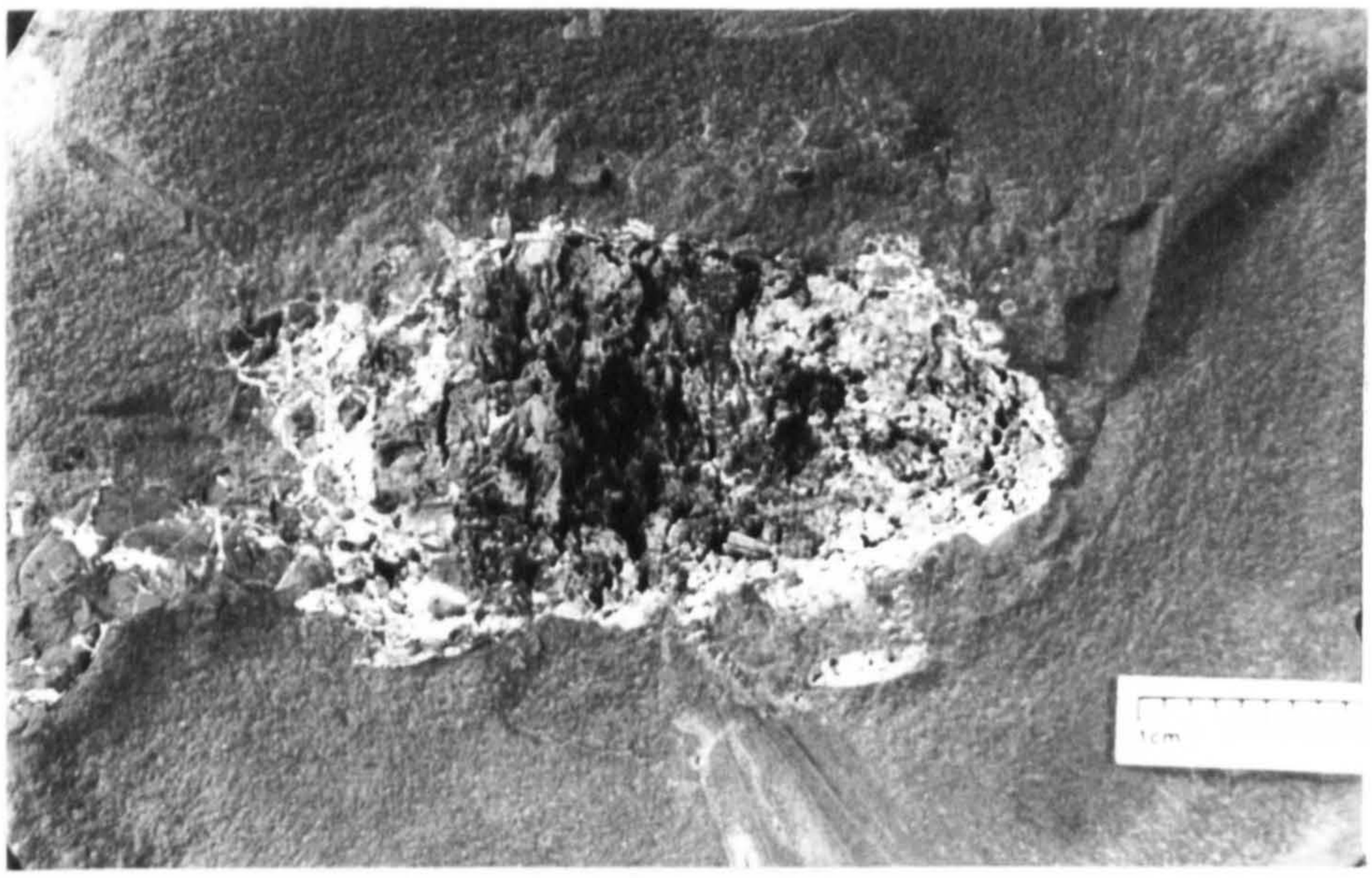


Plate 4.1A Indeterminate protorthopteran (FMNH PE29773), from which material was removed for X-ray diffraction analysis. Specimen recovered from Pit 11, Peabody Coal Company, Illinois. [Field Museum of Natural History (Chicago)].

Plate 4.1B Mazon Creek insects. A, Indeterminate protorthopteran with mineral-lined body cavity (FMNH PE32054). B, Indeterminate blattoid wing dissected by calcite septaria (FMNH PE27623). Specimens recovered from Pit 11, Peabody Coal Company, Illinois. [Field Museum of Natural History (Chicago)]

A



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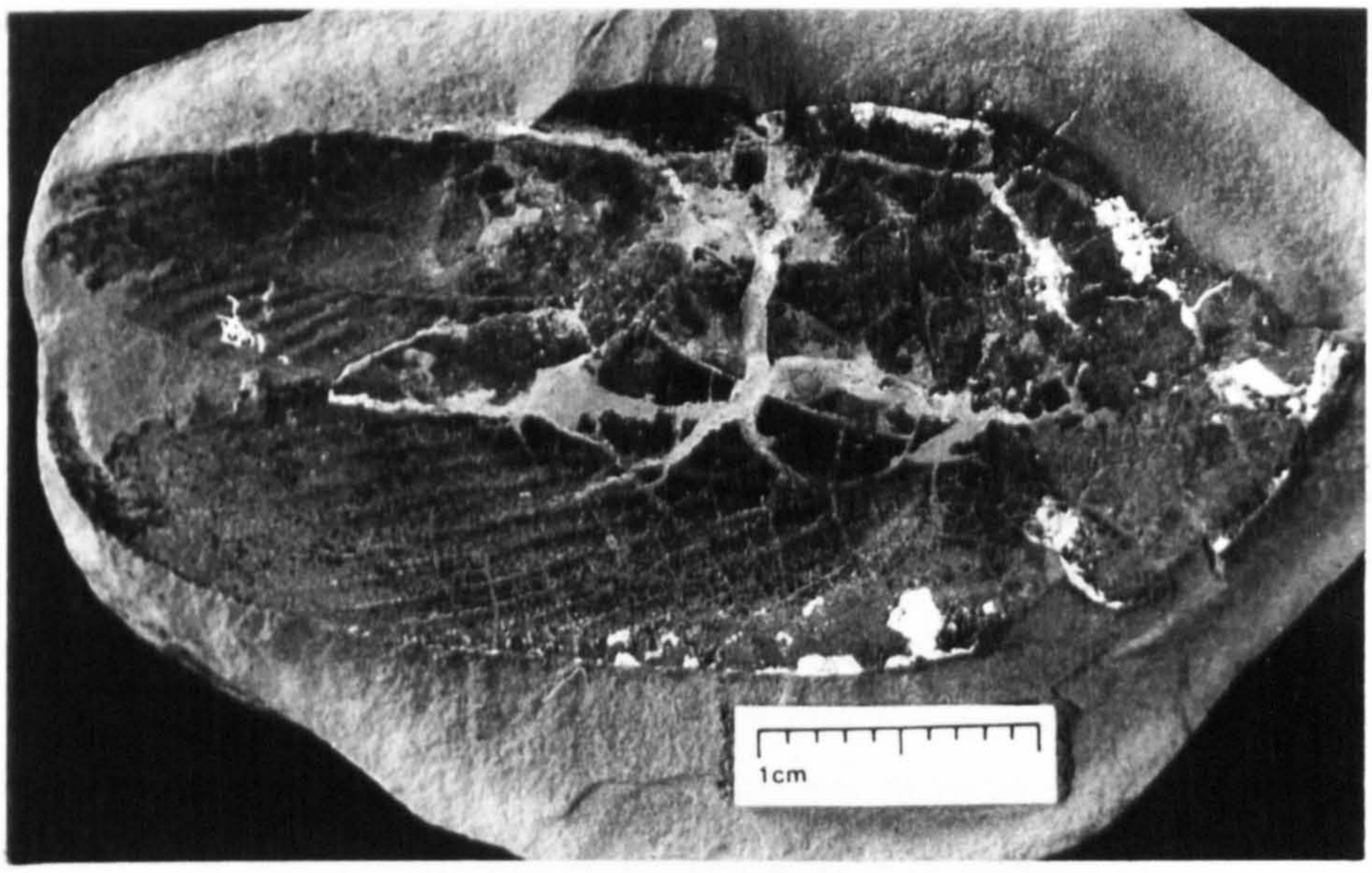


Scanning electron microscopy (Appendix A1.1). Each specimen was examined, uncoated, under the SEM. This necessitated a low voltage in order to reduce charging but still produced images of poor quality. However, these images allowed the most interesting mineralogical specimens to be identified, eliminating the need to coat all the fossils for investigation. Three specimens (of which one comprised both part and counterpart) were coated and examined under the SEM.

X-ray diffraction (Appendix A1.3). A single specimen (FMNH PE29773), including both part (Plate 4.1) and counterpart, was selected for study. Under the light microscope, four distinct minerals were identified on the basis of colour: white, creamy yellow, black and brown. The other mineralized specimens possessed a similar suite of minerals. Samples of these minerals were excavated from the 'part' using a fine scalpel, taking care to extract just one mineral. Samples of the concretion were also excavated in a traverse from periphery to fossil core.

Elemental Mapping (Appendix A1.2.1). The use of an energy dispersive system (EDS) of elemental mapping attached to an electron microprobe is still a relatively new procedure (see Martill *et al.* 1992). The technique allows the elemental composition of a particular region of a fossil, or the entire fossil, to be mapped, and their inter-relationships determined.

The method is most successful when conducted upon polished surfaces which reduce topographic distortion. However, since permission was granted only for non-destructive analyses, a relatively level region of the fossil was selected to minimise this effect. The specimen was carbon coated to avoid unnecessary peaks on the spectrum.

Elemental mapping is at its most powerful when used in conjunction with X-ray diffraction, since elemental assemblages indicative of particular minerals can be sought with some certainty. The specimen to be mapped was the counterpart of FMNH PE29773, from which mineral fragments had been removed for XRD analysis. Minerals noted by other authors (notably Woodland and Stenstrom 1979) also provided a useful guide. In total, seven elements were mapped: P, Ca, Zn, S, Fe, K and Si.

Using Adobe Photo-shop, an Apple MacIntosh image analysis package, it is possible to combine individual maps through a layering process, to produce a series of composite maps which allow the inter-relationship of the minerals to be examined.

4.5.3 Results

4.5.3.1 Structural preservation. No original internal structure was noted during SEM analysis, indeed recognition of the ventral/dorsal surface or anterior/posterior position was impossible in most cases except where a wing extended beyond the body.

The wings themselves are preserved only as impressions within the matrix. No organic material or mineral growth was noted.

Within the mineral melange, only the 'black' and 'white' minerals displayed recognizable boundaries. The relationship between the other minerals was impossible to discern under a secondary electron beam. The use of backscatter electrons to highlight mineral variation was hampered by the uneven texture of the fossil. There is no evidence of mineral replication of particular organs or body tissues.

4.5.3.2 General mineralogy. The concretions are composed primarily of siderite ($FeCO_3$) (Fig 4.03a). There is also a significant clay component, predominantly kaolinite ($Al_4[Si_4O_{10}](OH)_8$ and chlorite $(Mg,Al,Fe)_{12}[(Si,Al)_8O_{20}](OH)_{16}$) as well as subsidiary silica (SiO_2). There is no apparent compositional variation from the periphery to the fossil core noted in of any of the concretions.

The presence of four minerals within the body cavity was confirmed (Fig. 4.03a-d): the black mineral is sphalerite (ZnS); the white mineral, calcite ($CaCO_3$); the brown mineral, siderite. However, there is no single creamy yellow mineral. It is in fact a mixture of calcite and hydroxyapatite ($Ca_5[PO_4]_3OH$) (Fig. 4.02d). The fact that calcite is noted both alone with definite boundaries and as a mixture with hydroxyapatite might suggest two distinct phases of calcite mineralization. It may also suggest the diagenetic replacement of apatite by calcite.

4.5.3.3 Mineral maps. Elemental maps of a region 1x1cm of FMNH PE29773 (counterpart) are displayed in Figs 4.04a-g. Using the information gained from the earlier XRD analysis of the 'part' of the same specimen it is possible to ascribe a particular mineralogy to each elemental map.

The maps of zinc (Fig. 4.04c) and sulphur (Fig. 4.04d) cover almost exactly the same area, that of the mineral sphalerite (ZnS). Of the minerals revealed by XRD analysis, phosphorus (Fig. 4.04a) is found only in hydroxyapatite. The map of calcium encompasses both apatite and calcite (Fig. 4.03b).

Interpretation of the other maps is problematic. No potassium-bearing mineral was noted during examination of the XRD results. However, Woodland and Stenstrom (1979) noted the presence of illite ($K_{1-1.5}Al_4[Si_{7-6.5}Al_{1-1.5}O_{20}](OH)_4$) a potassium-bearing clay, in a number of specimens (Fig. 4.04g). The disseminated nature and limited quantity of the mineral may have masked its appearance on any XRD spectra.

Silicon is noted throughout the interior of the specimen (Fig. 4.04f), suggesting either the presence of silica alone, or it inclusion in various clays such as chlorite, illite or kaolinite (noted during XRD analysis: see also Woodland and Stenstrom 1979). The interpretation of the map of iron (Fig. 4.04e) is also problematic, since Fe is noted in both siderite and in chlorite.

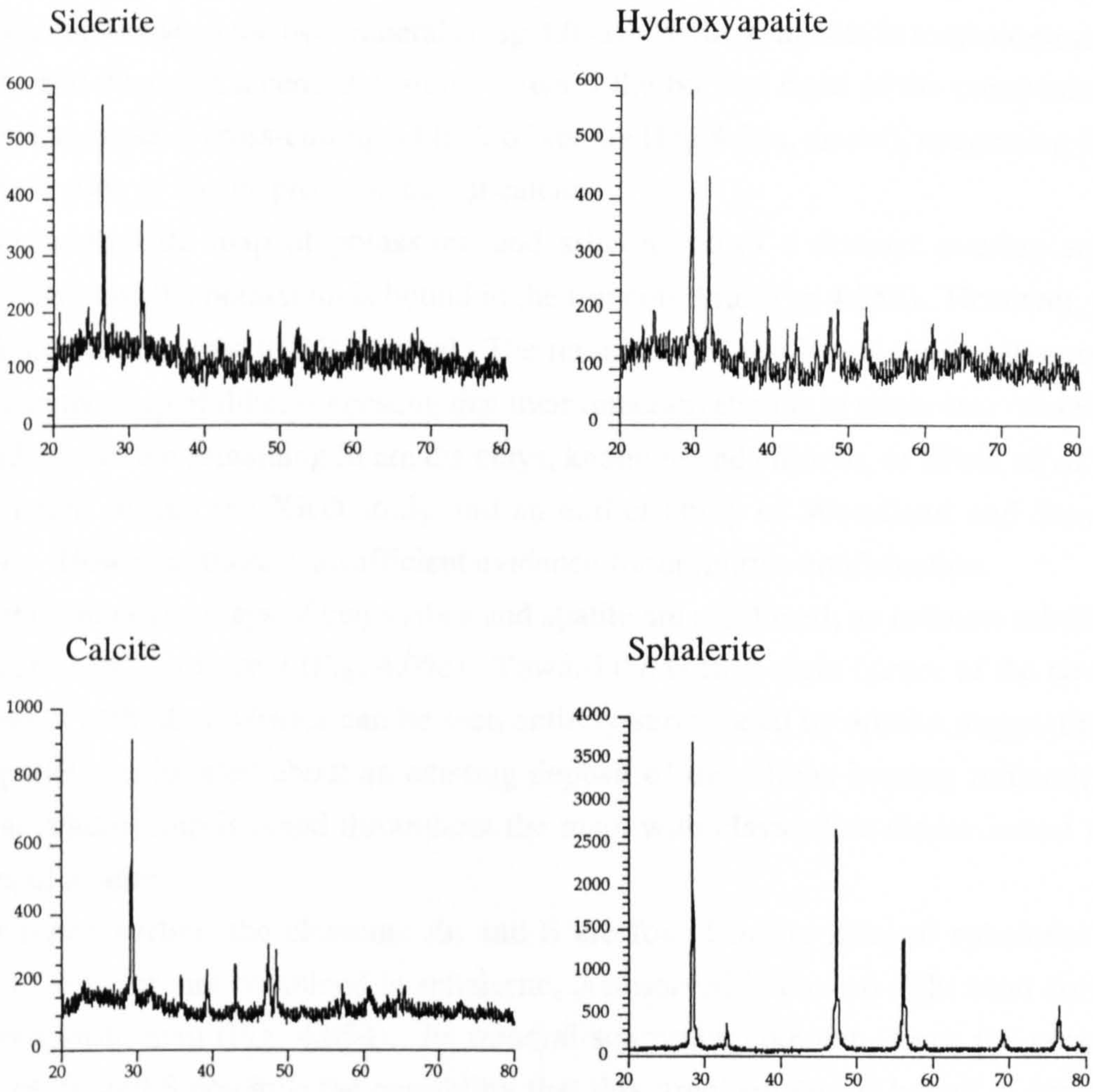


Figure 4.03 X-ray diffraction traces of the minerals from within body cavity of Mazon Creek fossil (see Plate 4.1, calcite - white; sphalerite - black; siderite - brown; apatite - cream).

The composite map of hydroxyapatite (P) and calcite (Ca) clearly delineates the relationship between the two minerals (Fig.4.05a). Hydroxyapatite is more common than calcite and occupies a central region. Toward the bottom right of the composite map, calcite can be seen cross-cutting a block of apatite (Fig 4.05a, arrow), suggesting that the mineralization of apatite preceded that of calcite.

The composite map of potassium and silicon shows a distinct overlap strongly suggesting that the potassium is bound in the mineral illite (Fig 4.05b). However, not all the silicon is restricted to this mineral. The remaining Si displays a similar disseminated nature to the map of illite, suggesting that their mineralization is in some way related. The candidates for the remaining Si are the clays, kaolinite and chlorite, or silica, all of which were noted during the XRD study and an earlier study of Woodland and Stenstrom (1979). However, there is insufficient evidence for definitive confirmation.

If the composite maps of clays/silica and apatite are combined, an intimate relationship between them is apparent (Fig. 4.05c). Toward the bottom right corner of the new map (arrow), a bleb of clay/silica can be seen entirely surrounded by apatite, suggesting that the apatite precipitated about an existing deposit of the silicon bearing mineral(s). A similar relationship is noted throughout the map, with clays/silica disseminated within bodies of apatite.

As noted earlier, the elements Zn and S are found in the mineral sphalerite (Fig. 4.05d). Sulphur, not combined in sphalerite, is observed in the top right hand corner of the composite map (Fig. 4.05d). Its mineral source is unknown, since the combined maps of Zn and S preclude the possibility that this 'free' sulphur is bound in sphalerite. Iron can be seen disseminated throughout the interior of the specimen in a similar fashion to the clay elements and silica but does not overlap with sulphur, suggesting that the element may not be bound in siderite, but perhaps in chlorite (Fig. 4.05e: see Woodland and Stenstrom 1979).

If all the elemental maps are combined, a single complete image is produced (Fig 4.06), which represents all the minerals present. The fact that sphalerite is a late stage mineral is indicated not just by its peripheral position, but by the fact that it completely surrounds a number of other minerals (see Fig. 4.06).

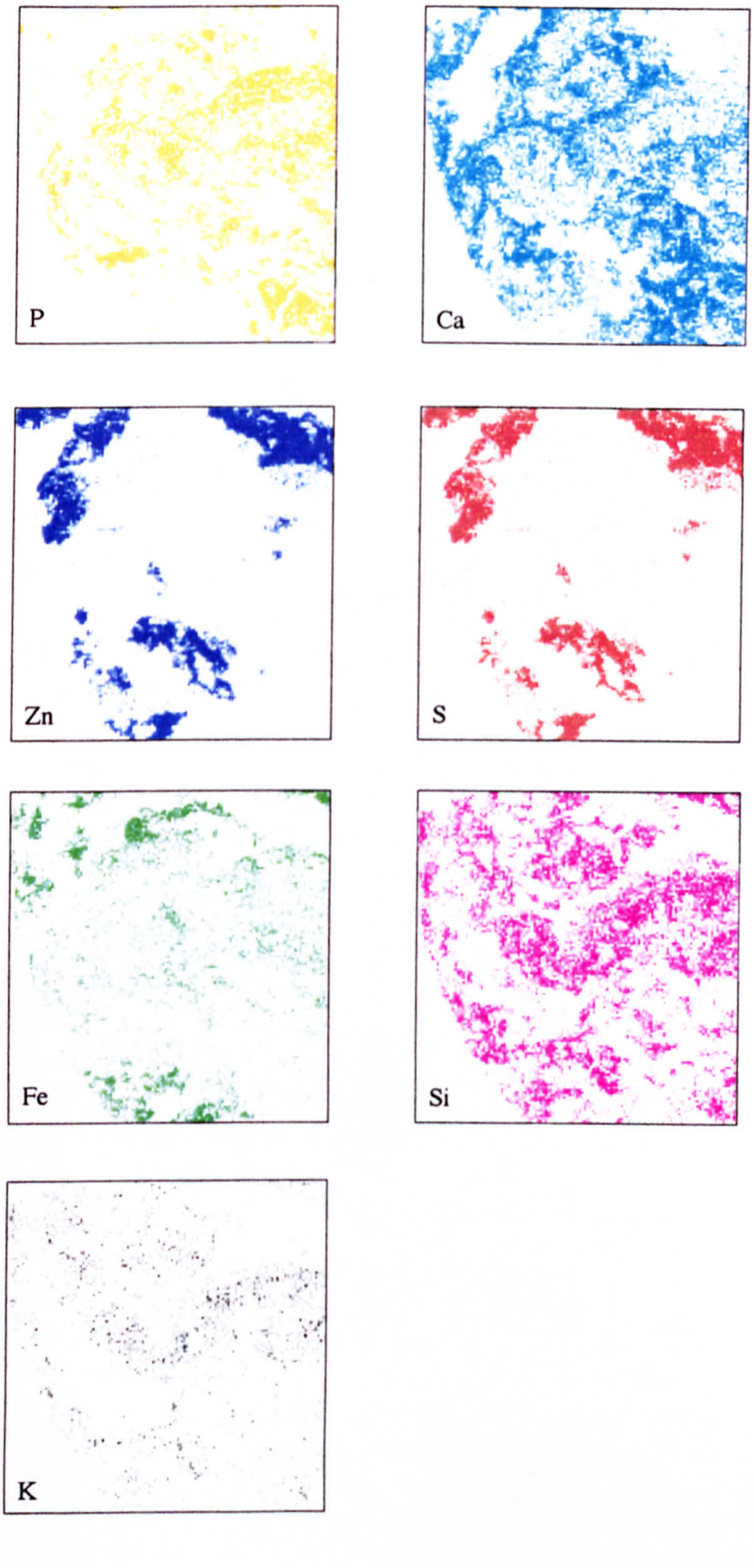


Figure 4.04 Elemental maps of common region of a protorthopteran (FMNH PE32054). Each box is 1x1cm.

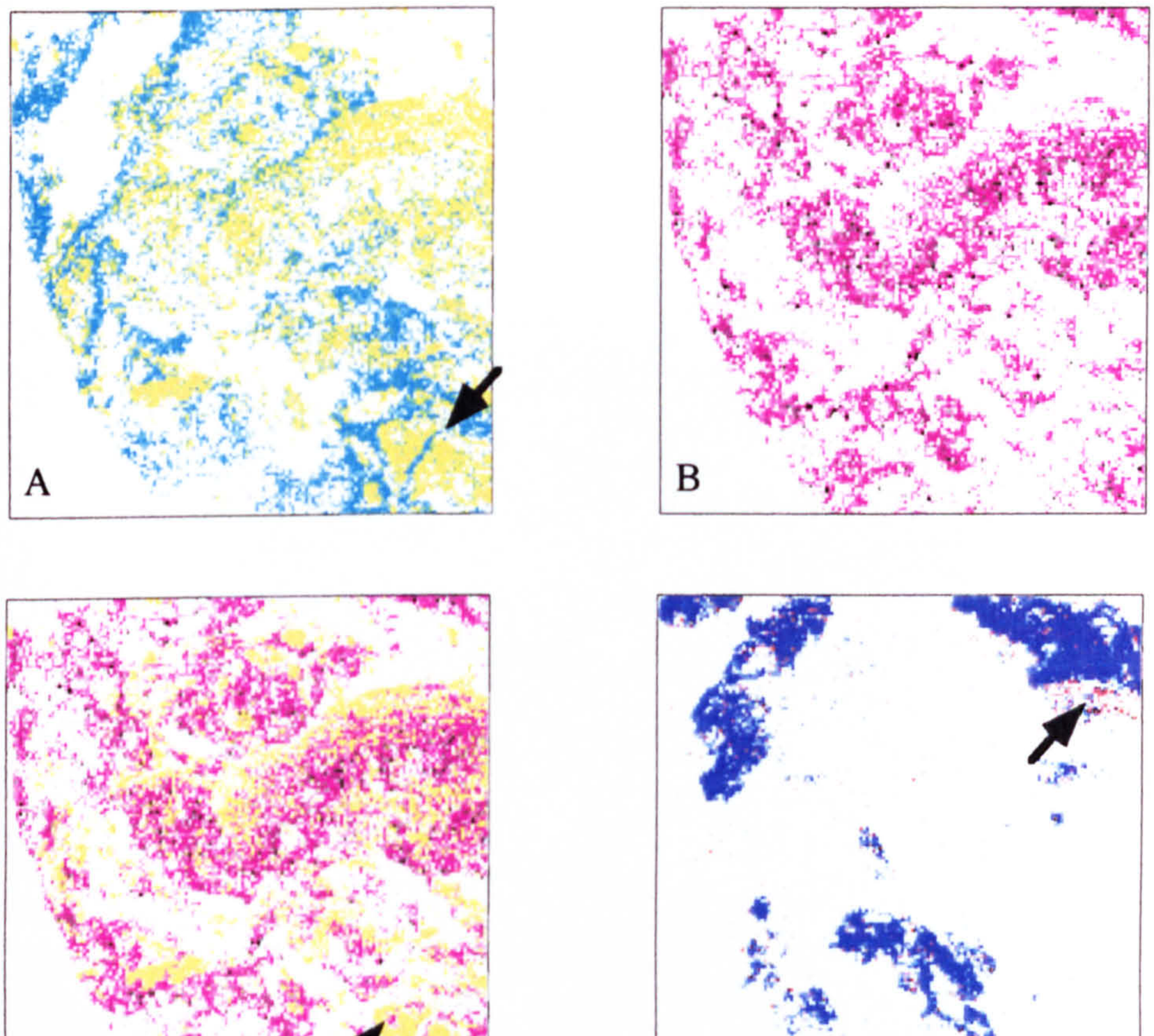


Figure 4.05 Mineral maps of protorthopteran (see Fig. 4.04). A, apatite (yellow) and calcite (blue). Arrow indicates calcite cross-cutting apatite. B, clay (grey) and silica (pink). C, clay (pink) and apatite (yellow). Arrow indicates enclosure of clay within apatite. D, Sphalerite (blue) and free sulphur (arrowed). E, iron [siderite or ?chlorite] (green) and clay (pink/grey).

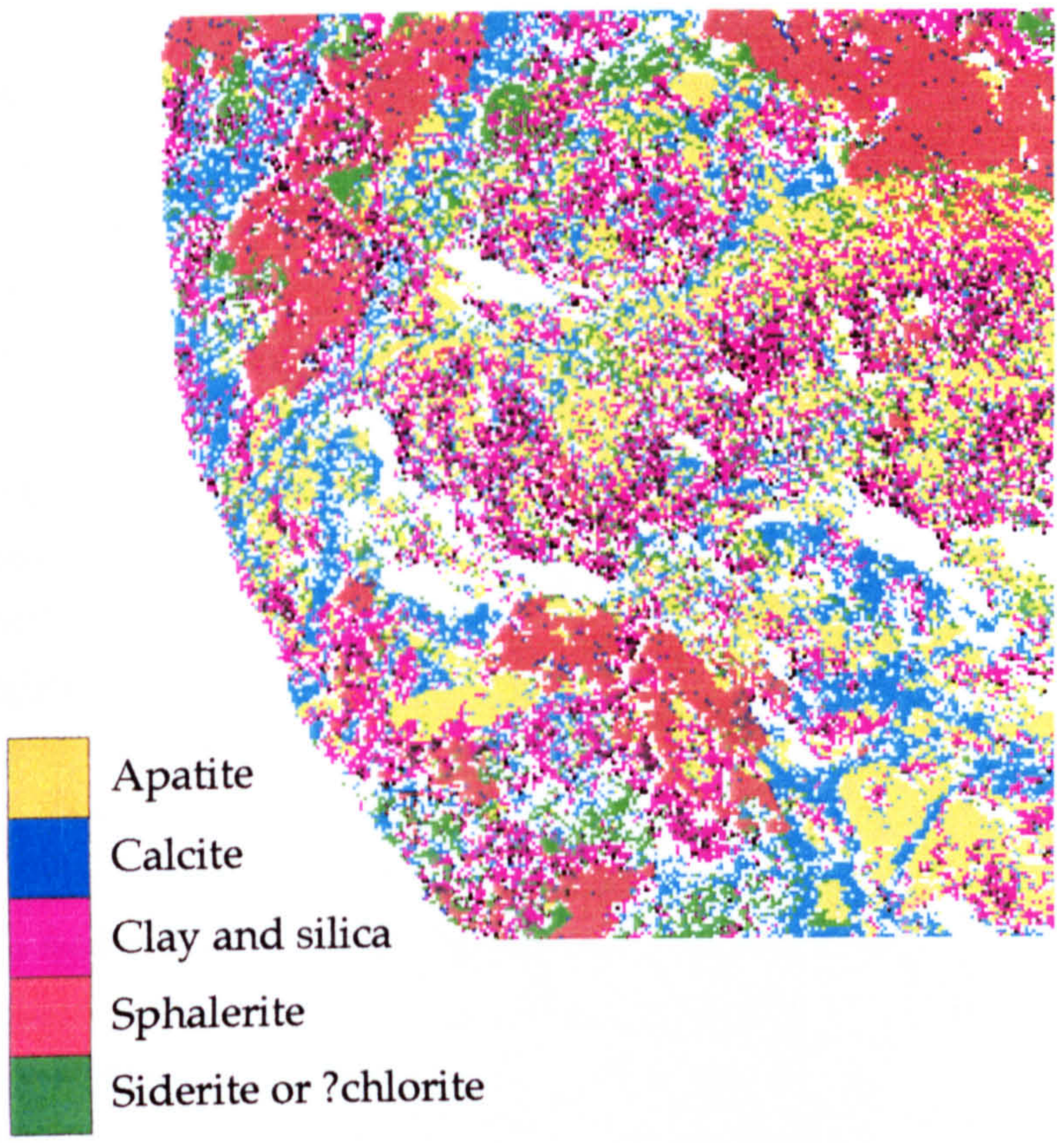


Figure 4.06 Composite map showing major minerals. White patches within map are topographic lows. The curved left-hand boundary is a shadow-effect and is not the periphery of the concretion.

PAGE NUMBERING AS ORIGINAL

4.5.4 Discussion

The Mazon Creek concretions must have begun to form before decay completely destroyed the carcass. The preservation of traces of labile tissues such as those of jellyfish, and the yolk sacs of larval fish, indicate early mineralization. Colour markings on bivalves and insects, setae on worms, and the radulae of both chitons and cephalopods have been advanced as evidence of limited decay (Woodland and Stenstrom 1979). However, these features are relatively decay resistant and consequently provide less definitive evidence of the timing of decay and mineralization.

Despite this, scanning electron microscopy (of 11 specimens) failed to reveal mineral replication of any original organic structures. The lack of internal structure may be due to its loss prior to mineralisation, *i.e.* decay had progressed to a least stage 2 (see Chapter 2). Soft tissue is rapidly broken down, and the internal structure reduced to an amorphous 'sludge' occupying the lowermost region of the recalcitrant cuticle sac. The cuticle sac can persist for considerable periods of time, slowly leaking internal material before the commencement of the next stage (disintegration of abdomen and loss of appendages: Chapter 2). If mineralisation at Mazon Creek began post stage 2, then any mineral would have precipitated into a cuticle sac devoid of internal tissue.

The presence of structureless clay minerals and silica within the interior region of the fossil, would seem to confirm the absence of such internal material. The enclosing sediment is composed predominantly of illite (40-50%), kaolinite (15-25%), chlorite and quartz (14-30%) (Shabica 1971; Woodland and Stenstrom 1979). Woodland and Stenstrom 1979 consider the kaolinite to be the alteration product of illite formed late in the diagenetic sequence. However, authigenic kaolinite has also been reported from plant-bearing concretions (Hughes 1970; Boher and Hughes 1971). Gabbott *et al.* (1995), examing the conodont of the Soom Shale, South Africa, have proposed that direct precipitation of clay can replicate soft tissue. However, the Mazon Creek fossils display no evidence of soft part preservation by such means. Whether the clays of the Mazon Creek are primary, introduced through rupture in the cuticle, or are secondary, resulting from mobilization of the appropriate ions (see Gabbott *et al.* 1995) cannot be answered with the evidence currently available.

The interior of the fossil is dominated by hydroxyapatite and calcite. The occurrence of clay minerals within apatite blocks suggests that their introduction preceded (or was contemporaneous with) phosphate precipitation. The cross-cutting nature of the calcite with respect to apatite indicates that of these minerals, apatite precipitated first. Apatite is perhaps the most important authigenic mineral in the replacement of soft tissue, both in terms of fidelity of preservation (see Martill 1988; Wilby 1993; Wilby and Whyte 1995; Duncan and Briggs 1996) and frequency (Allison 1988c; Allison and Briggs 1991). Experimental evidence indicates that apatite precipitation can be very rapid indeed (Martill and Harper 1990; Briggs and Kear 1993a,b, 1994). If mineralization occurred over a similar time frame in the Mazon Creek fossils, then replication of internal tissue by the

authigenic minerals would be expected. The absence of such tissue replication would appear to be further evidence for the lack of such tissue when mineralization commenced.

The control on the precipitation of calcium carbonate (calcite) or calcium phosphate (apatite) has been likened to a 'switch' with the default set for the precipitation of $CaCO_3$ (Allison 1988c). In order to facilitate the phosphatization noted at Mazon Creek, this switch must be turned 'off'. The position of the switch, and the resultant mineralisation, is strongly influenced by microbial activity (Briggs and Wilby 1996). Laboratory investigation of the influence of decaying matter using shrimps (Briggs and Kear 1994) revealed the major control to be decay-induced pH which in turn affects the relative concentrations of HCO_3^- and phosphate produced (directly or indirectly) as by-products (Berner 1968; Briggs and Kear 1994). In experiments where the initial acidic by-products of microbial metabolism (such as CO_2 and H_2S) escaped by diffusion ('open' conditions), the pH remained predominantly alkaline and $CaCO_3$ was precipitated. Where the experiment was completely 'closed' and anoxic, a pronounced and persistent fall in the pH resulted in the switch favouring the precipitation of apatite. Minor variations in the parameters can affect the switch position (see Burton and Walter 1990; Dove and Hochella 1993). The influence of pH is localized; different minerals may form in different parts of the same decaying carcass (see Briggs and Kear 1993a). The control is also dynamic. In some longer running experiments, tissue was first phosphatized and then overgrown by $CaCO_3$, reflecting a gradual rise in pH following initial decay (Briggs and Kear 1994).

In the fossils of the Mazon Creek, precipitation of phosphate may have been favoured by the onset of early concretionary growth which, effectively closed the system. As the amorphous internal material continued to break down a persistent fall in the pH would flick the switch to phosphate, hence apatite would infill the body cavity. The source of the phosphate ions may have been the decomposing organic matter (Lucas and Prévôt 1984; Prévôt and Lucas 1986). Within aerobic sediment, these ions can then be adsorbed to ferric hydroxides (Benmore *et al.* 1983). Reduction of these ferric hydroxides at the anoxic/oxic interface can liberate phosphates to solution which are then concentrated in the decomposing carcass (Benmore *et al.* 1983).

Since calcium carbonate is found filling fractures in blocks of the apatite, the switch must have returned to the default condition. Following initial decay and the concomitant fall in pH favouring apatite, continued decay would drive the pH back up, so returning the 'switch' to the default position, and precipitating $CaCO_3$ (see the experiments of Briggs and Kear 1994, for an analogue). However, it is unlikely that the volume of bicarbonate generated by the decay of a macro-organism would be sufficient to produce the volume of carbonate noted in the Mazon Creek concretions (Raiswell 1971, 1976). Additional bicarbonate ions may have migrated upwards from the underlying, decomposing peat (Colchester Coal), and nucleated about the decomposing carcasses.

The precipitation of sphalerite must have occurred after the infilling of the carcass by earlier mineralization, since inclusions of various minerals are noted within the discrete units of sphalerite (see above). The source of zinc may have been marine waters, suggesting a late stage influx (see Moore *et al.* 1992, for a modern anologue).

4.6 IMPLICATIONS

4.6.1 Previous models

Allison (1988d) stated that the haematite coating the surface of plants and soft-bodied animals was the first mineral phase to form. Since haematite is only ever precipitated in oxidising conditions he concluded that it must have formed during the initial aerobic stages of burial. Woodland and Stenstrom (1979) consider that in some instances the aerobic decay of organic matter in the presence of a small amount of sulphate (produced by sulphate-reducing bacteria) and iron would lead to the precipitation of iron sulphide and, where sufficient sulphur itself is present, pyrite.

Both Woodland and Stenstrom (1979) and Allison (1988d) state that, upon the exhaustion of free oxygen and with burial, decay proceded anaerobically. As decomposition progressed, the release of CO_2 lead ultimately to an enrichment of bicarbonate ions. Both groups consider this source of bicarbonate ions to be insufficient for carbonate formation and invoke the migration of such ions from decomposition of the underlying peat (later to become the Colchester Coal). The high levels of iron in fresh water environments would have fovoured the precipitation of siderite (Berner 1971, 1981). It is generally agreed that siderite started to form while the sediment porosity was high (Woodland and Stenstrom 1979; Berner 1968; Allison 1988d), perhaphs within 5m of the surface (Greensmith 1978).

Woodland and Stenstrom (1979) considered the infilling of the fossil body cavity by minerals (pyrite, calcite, sometimes kaolinite, occasionally sphalerite and rarely galena), to reflect a late stage mobilisation of sulfide, either by bacterial activity on migrating sulfate-charged waters, or the migration of the sulphide ion itself from the underlying peat (caused by compaction-induced expulsion of instertitial fluids). Baird *et al.* (1986) state that pyrite formation was due to the liberation of sulphide ions produced during the decay of sulphur-containing proteins such as cysteine. However, Allison (1988d) disagreed, countering that the sulphur content of these proteins was too low (<1%) and therefore insufficient to produce the volume of sulphides noted in the the pyrite. He considered marine pore-waters a more likely source (see Moore *et al.* 1992, for modern analogue).

4.6.2 New model

The extent to which the mineralization of the insect fossils applies to the Mazon Creek fossils at large is unknown. To date no author has noted the presence of apatite in *any* fossil from this deposit. Apatite, particularly if associated with calcite, is virtually

impossible to identify in hand specimen and is often masked by calcite during XRD analysis. It may be that where calcite has been reported apatite may be discovered.

No model has suggested that mineralization may occur within the decaying carcass prior to the instigation of concretion growth. Could this explain the failure to find siderite concreting about non-mineralised nuclei in the recent concretions of Norfolk and the Mississippi Delta? Clearly the comparison between ancient and modern concretions is problematic. It may be that authigenic apatite and calcite play an important role in the early fossilization process, and thus the failure of modern analogues stems from the absence of such minerals.

Calcite precipitation in the Mazon Creek fossils has always been considered a late stage phenomenon, often attributed to a change in the pore water chemistry. No author has suggested that the precipitation of calcite may result from the flicking of the apatite/calcite 'swich' early in the diagenetic history. The above findings suggest that their are two phases of mineralization, both of which initially stem from the decay of the carcass: internal apatite and calcite precipitation and the development of the concretion. Decay of the carcass would have driven down the pH within the closed carcass favouring apatite precipitation, while outside the carcass the escape of decay by-products such as CO_2 and H_2S would have favoured the precipitation of siderite (since the high iron content of the pore water would have precluded the development of calcite: Berner 1971). As the pH within the carcass rose after initial decay and concretion development, the switch would then favour calcite precipitation within the carcass. Additional Ca^{2+} could have been supplied by cation exchange as the illite broke down into kaolinite (Woodland and Stenstrom 1979). This early internal mineralization may be responsible for the common three-dimensionality noted in the Mazon Creek insects (see Allison & Pye 1994)

Alteration of the pore water chemistry following a marine inundation (see Moore *et al* 1992, for a modern analogue) would still be responsible for the infilling of the fossil-bound voids with such late stage sulphides as sphalerite and galena (as envisaged by all authors thus far).

CHAPTER 5

WEALD

5.1 INTRODUCTION

One of the most significant Cretaceous insect deposits is the Weald Clay of the Weald, southeastern England (Hauterivian - Barremian/?early Aptian: Allen 1990) (Jarzembowski 1991a). The insects occur in sideritic and phosphatic lenses within clay beds commercially quarried for brick production (Jarzembowski 1991a). The majority of specimens have been recovered from two working pits, Keymer (Cook and Ross 1996) and Smokejacks (Cook 1996), and a disused third, Auclaye (Jarzembowski 1991a). Slabs from a fourth pit, Clockhouse, now reclaimed, have been gathered together in a rock store and designated a Site of Special Scientific Interest (Ross 1992; Cook 1997).

5.1.1 Aims and scope of work

While a number of papers have detailed the taxonomy of the Wealden insects (*e.g.* Jarzembowski 1977, 1984, 1991b) their taphonomy has remained unstudied. The stratigraphy of some of the Wealden clay pits has recently been documented (Ross and Cook 1995; Cook and Ross 1996; Cook 1997) and work has begun on the taphonomy of the vertebrates (Cook 1995a, b). The discovery of a large insect-bearing lens during the logging of the Smokejacks pit (A.J. Ross, *pers. comm.*), provided an opportunity to examine and document the taphonomy of the stratigraphically constrained insect fauna. The taxonomy of the insects is the subject of a study by Andrew J. Ross of the Natural History Museum (London).

5.1.2 Previous studies

Insects were first reported from the Weald in 1854 (Binfield and Binfield 1854). However, their small size and fragmentary nature ensured that the insect biota would remain virtually unknown for much of the next century (Jarzembowski 1977). Only occasional descriptions of individual species (*e.g.* cixiid bug: Fennah 1961; aculeate wasp: Evans 1969) or their traces (curculionid traces in wood: Blair 1943) were published during this period. In the 1970s, Wealden palaeoentomology experienced a renaissance, with the work of Jarzembowski (1977, 1984, 1991a, b, 1995). Jarzembowski initiated a number of collecting trips to the various pits (*e.g.* Jarzembowski 1991a) and published a number of descriptions of various insect species (*e.g.* Jarzembowski 1981, 1984, 1989b, 1991b). Useful taxonomic lists have been produced

subsequently by Ross and Cook (Ross and Cook 1995; Cook and Ross 1996; Cook 1996).

5.2 GEOLOGICAL SETTING

5.2.1 Introduction

Early Cretaceous sedimentation in Europe was controlled by a series of structural basins, including the Weald Basin of southern England, which covered much of Kent, Surrey, Sussex and northern Hampshire (Fig 5.01) (Kirkaldy 1963; Morter 1984; Lake and Shepard-Thorn 1987). The basin may have been connected to those of the continent, but this has not been proved (Kaye 1966).

The sediments of the Weald Basin form a large anticline (Fig. 5.01). The Hastings Beds of the core are arenaceous in character, with minor units of mottled clay (Fig. 5.02). The flanking Weald Clay consists of a sequence of soft grey clays and siltstones which weather to mottled yellow, and minor beds of sandstone and limestone. Insects are recovered from the sideritic and phosphatic lenses that occur throughout the sequence (Jarzembowski 1991; Ross and Cook 1995). The unit reaches a thickness of some 700m in the west, and thins eastward (Jarzembowski 1991b). Lake and Shepard-Thorn (1987) review the Lower Cretaceous sediments of southern England.

The insects of this study were recovered from the Smokejacks Brickworks pit, Surrey (Fig. 5.01). The sediments of Smokejacks are amongst the youngest sediments sampled by any pit of the Weald and belong to the Upper Weald Clay (Barremian, 131.8-124.5Ma; Fig 5.02).

5.2.2 Palaeoenvironment

During the late Berriasian, tectonic activity and increased precipitation led to the formation of a number of major rivers which drained into the Weald Basin. The resulting deposition of fluvial sandstones, overbank silts and clays constitutes the Hastings Beds (Allen 1981, 1990; Hancock and Rawson 1992; Fig. 5.02). By earliest Hauterivian, a decline in tectonic activity led to a switch from arenaceous sedimentation to the deposition of the argillaceous Weald Clay (and the Wessex Formation of the Isle of Wight: Lake and Shepard-Thorn 1987). The Weald Clay is the non-marine product of the old age phase of a significant river(s) deposited in a subsiding basin (Allen 1981, 1990; Cook and Ross 1996). The depositional environment has been variously interpreted as a transgressive delta front (Allen 1959; Taylor 1963) or a braidplain of interconnecting rivers, fans and small water bodies (Allen 1981; Jarzembowski 1991a). From this period to the mid Hauterivian, northwestern Europe experienced several transgressive/regressive cycles, and the resulting sediments display large-scale cyclicity (Cook 1995b). Two well-developed cyclothems have been identified in the Wealden sediments (Worssam 1978), although a third has been suggested (Allen 1959). Occasional quasi-marine bands are evidence of marine high stands (Hancock and Rawson 1992). By Late Wealden times

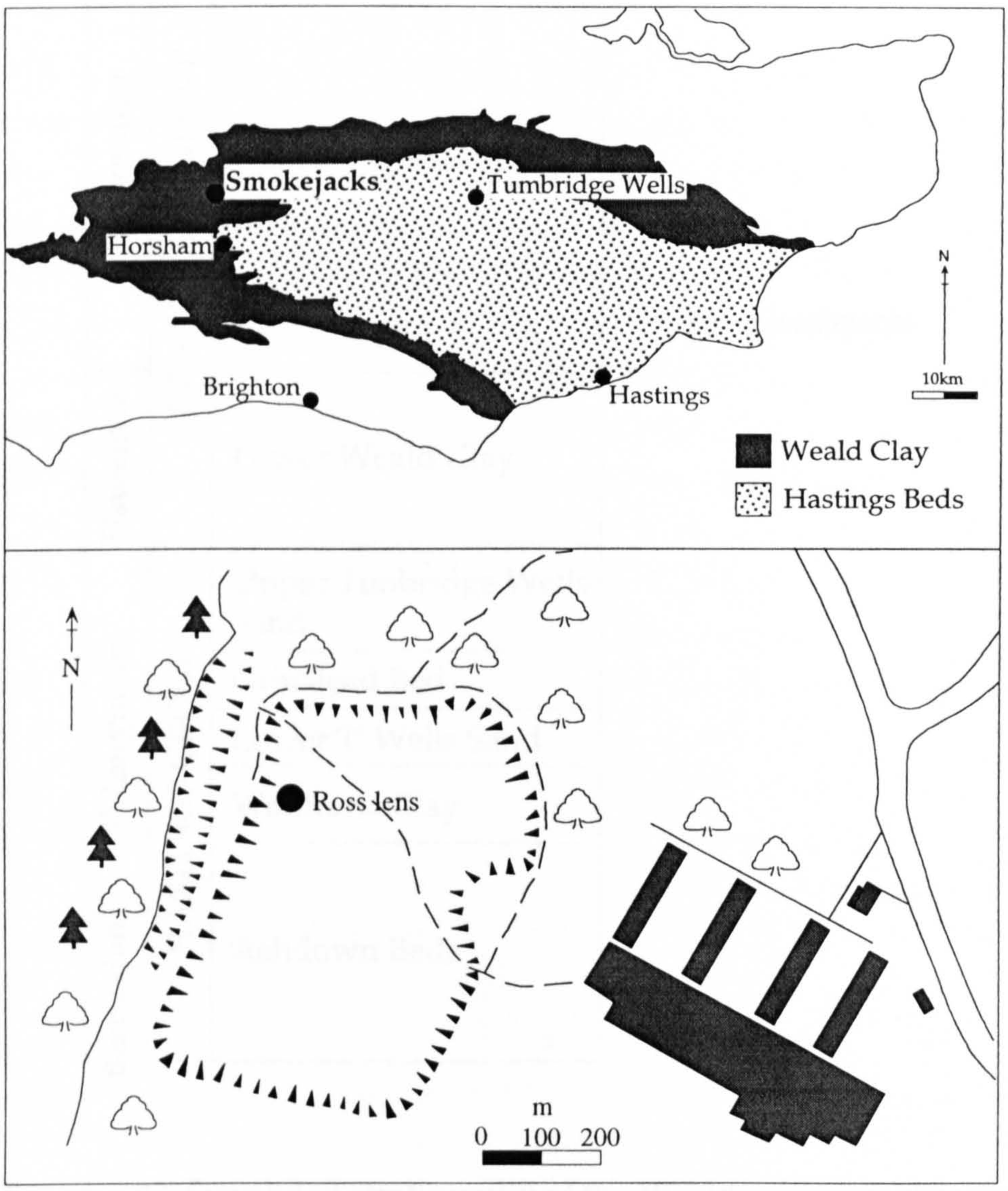


Figure 5.01 A Outcrop of Weald Clay and Hastings Beds. Location of Smokejacks Brickworks. **B** Smokejacks Brickworks pit. Approximate position of fossiliferous 'Ross Lens' (see Fig. 5.03). (Both maps courtesy of Liz Cook, Bristol University).

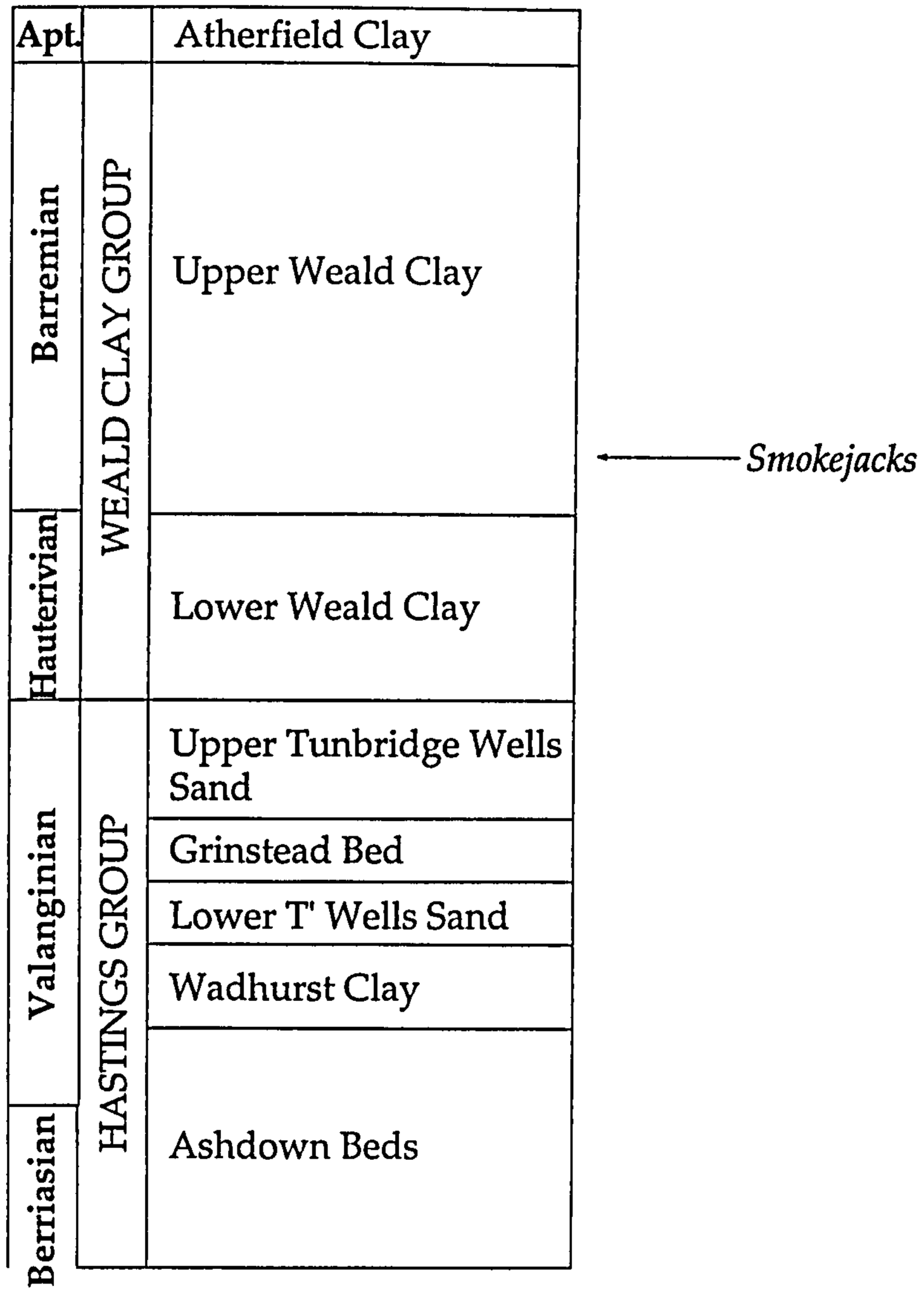


Figure 5.02 Simplified stratigraphy of the Wealden Group, showing the position of the Smokejacks pit. Abbreviations: Apt., Aptian. (A.J. Ross, *pers. comm.*).

the Weald and Wessex basins had united, although two depocentres remained (Allen 1972).

5.2.3 Palaeoclimate

During the early Cretaceous, southern England was positioned ~30° north of the Equator (Smith and Briden 1977). The general mineralogy of the Weald Clay and the occurrence of calcretes suggest arid conditions (Ruffel and Batten 1990). The flora of the Weald is adapted to dry conditions: small leaves, thickened leaf cuticles, sunken stomata and tightly packed sporangia are features consistent with conditions of high insolation and water stress or a halophytic mode of life (Batten 1974; Alvin 1974). However, the discovery of fungi indicates that the climate was at least periodically, or locally, humid (Alvin and Muir 1970; Alvin *et al.* 1981). Well-developed growth rings in the woody material indicate seasonality (Alvin *et al.* 1981) or a humid/arid cyclicity (Allen 1981).

Much of the plant material recovered from the Weald is fusainized, indicating pre-preservational burning (Alvin 1974). The quantity of such material suggests that forest fires were relatively common. Since such fires are most common during droughts today, a number of workers have inferred that southern England experience drought conditions during this period (Batten 1974; Alvin 1974; Alvin *et al.* 1981).

Jarzembowski (1984, 1991b) has used the discovery of termites in the Weald to constrain the temperature still further. Since modern termites tolerate a narrow range of conditions (tropical to temperate) (Emerson 1955; Weidner 1970), Jarzembowski has used the low species diversity of Wealden termites to suggest that they were living at the limit of their ecological range, *i.e.* warm temperate rather than tropical conditions (Jarzembowski 1991b). However a number of assumptions are inherent in this deduction: *i.e.* that ancient termites tolerated the same temperature range; and that the low diversity of Wealden termites is not a taphonomic artifact.

5.3 SMOKEJACKS

5.3.1 Introduction

Smokejacks Brickworks is approximately 10km northwest of Horsham, Surrey (Fig. 5.01). The sediments consist of a thick sequence of silty clays with few substantial sandstone beds. The fossils are recovered primarily from minor siderite and phosphate lenses. The stratigraphic sequence lies within the Upper Weald Clay Formation (Barremian: Fig. 5.02), just below the B.G.S. Nº 5c marker sandstone (Ross and Cook 1995).

5.3.2 Sedimentology and palaeoenvironmental interpretation

Twenty-three metres of sediment are exposed in the Smokejacks Brickworks pit (Fig. 5.03). Detailed logs have been published by Ross and Cook (1995). The section is dominated by grey clay, which is often mottled and can be quite silty. Minor shales are

noted throughout the section, but are stratigraphically more common in the south-east of the pit (Log 1: Ross and Cook 1995). Towards the top of the sequence, thick beds of sand (0.1-1m) and minor ironstone horizons (<0.2cm) occur (Fig. 5.03; Logs 2 and 3: Ross and Cook 1995). The insects are often concentrated in partings or thin layers within the sideritic and phosphatic lenses (Jarzembowski 1977). The insects of this study were recovered from a large (~2x0.8m) phosphatic lens, approximately 3.5m above the base of the section (Fig. 5.03).

The lowermost shales include fish and conchostracans indicative of shallow, fresh water, and isopods and ostracods suggestive of a marine influence (Fig 5.03: Ross and Cook 1995). Deposition was presumably in a shallow lake or lagoon with periodic marine incursions. The upper sandstone beds of the pit have yielded remains of dinosaurs and terrestrial plants. The fossils, together with the red/orange clays (Log 4: Ross and Cook 1995) indicate an emergent land surface and sub-aerial weathering. The change in lithology and fossil content up sequence has been interpreted as reflecting the transition from a lake or lagoon to a fluvial/mudplain environment (Ross and Cook 1995).

The insects commonly occur toward the base of sediment lenses in association with burrows, rootlet and stem casts, and clay casts (Jarzembowski 1991a; Cook and Ross 1996). The sediments and biogenic structures suggest these lenses represent deposition in overbank pools or abandoned channels, *i.e.* quiet waters, not part of the active channel system. The Ross lens, from which the insects for this study were recovered, represents such a feature

5.3.3 Biota

Twenty-two families of insect have been reported from the Smokejacks Brickworks (Table 5.1). Coleoptera and Blattodea dominate the biota (Fig 5.04). The Coleoptera are represented almost exclusively by elytra, a factor which has hampered their identification. Only two families have thus far been confirmed: Cupididae and Elateroidea. Continued study and identification may yet increase diversity. Cockroach tegmina are also common but venation-based taxonomy remains confused (see Chapter 2, section 2.5.1). To date, only the family Mesoblattinidae has been recognized. The living representatives of these coleopteran and blattodean families are associated with damp leaf-litter.

The other orders are markedly less common. Both Hemiptera (Homoptera: Cicadellidae, Fulgoroidea, Palaeontinidae; Heteroptera: Progonomocimicidae) and Orthoptera (Acridoidea, Elcanidae, Grylloidea, Hagloidea) occur, living representatives of which suggest woodland and meadow (Table 5.1). The families of Diptera (Mycetophilidae, Rhagionidae and Tipuloidea) and order Odonata are associated with moist wooded areas and still or slow flowing water. The orders Hymenoptera, Neuroptera, Mecoptera and Isoptera constitute only a minor component of the biota (Fig. 5.04). Trichoptera are known primarily from their agglomerated cases.

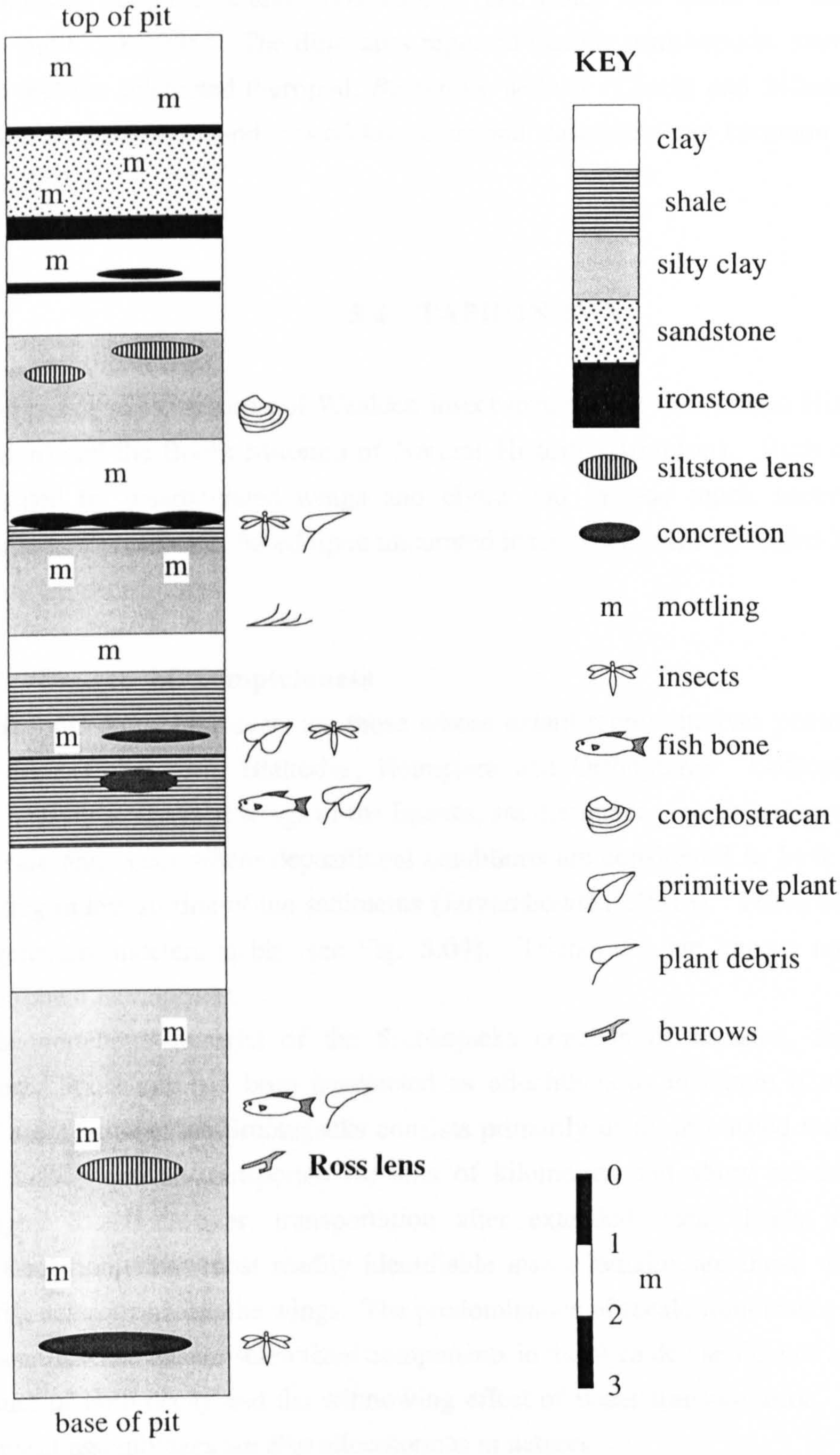


Figure 5.03 Lithostratigraphical log of Smokejacks Brickworks corresponding to log 2 of Ross and Cook (1995). The insects for this study were recovered from the Ross lens.

Other invertebrates include ostracods, isopods, conchostracans and bivalves (Jarzembowski 1991a). Vertebrate material consists predominantly of isolated teeth and fragments of bone (Ross and Cook 1995). The scales and bones of fish are common (Ross and Cook 1995). The dinosaurs reported include ornithopods, sauropods (Rivett 1953) and the celebrated theropod, *Baryonyx walkeri* (Charig and Milner 1986). The remains of pterosaurs and crocodiles occur and gastroliths are common (Rivett 1956; Cook 1995b).

5.4 TAPHONOMY

5.4.1 Introduction

The principal repositories of Wealden insect material are the Natural History Museum (London) and the Booth Museum of Natural History (Brighton). Both collections are dominated by disarticulated wings and elytra and include much material yet to be identified. This study is based upon uncurated insect specimens provided by the Natural History Museum.

5.4.2 Degree of completeness

The most common insects are those whose extant representatives possess sclerotized forewings (Coleoptera, Blattodea, Hemiptera and Orthoptera). Coleoptera, with the most heavily sclerotized wings of the Insecta, are dominant. Insect body components are very rare and occur where depositional conditions are considered to have been quieter, resulting in less sorting of the sediments (Jarzembowski 1991a). These body fragments are generally indeterminable (see Fig. 5.04). Trichoptera are known only from their more robust larval cases.

The vertebrate material of the Smokejacks consists of abraded, fragmented and scattered bones and has been interpreted as allochthonous in nature (Cook 1995a, b). The insect fauna of the Smokejacks consists primarily of disarticulated wings. Recently dead insects can be transported for tens of kilometres and show no evident damage (Chapter 3). However, transportation after extended decay leads to more rapid disarticulation. The most readily identifiable insect remains are those which are most heavily sclerotized, *i.e.* the wings. The predominance of recalcitrant insect fragments and the near absence of non-sclerotized components in the Wealden sediments is likely to be a product of both decay and the winnowing effect of water transportation, indicating that the insect assemblages are also allocthonous in nature.

The insects commonly occur toward the base of sediment lenses in association with burrows, rootlet and stem casts, and clay intra-clasts (Jarzembowski 1991a; Cook and Ross 1996). The sediments and biogenic structures suggest that deposition occurred in an overbank pool or abandoned channel, *i.e.* quiet waters isolated from the active channel system.

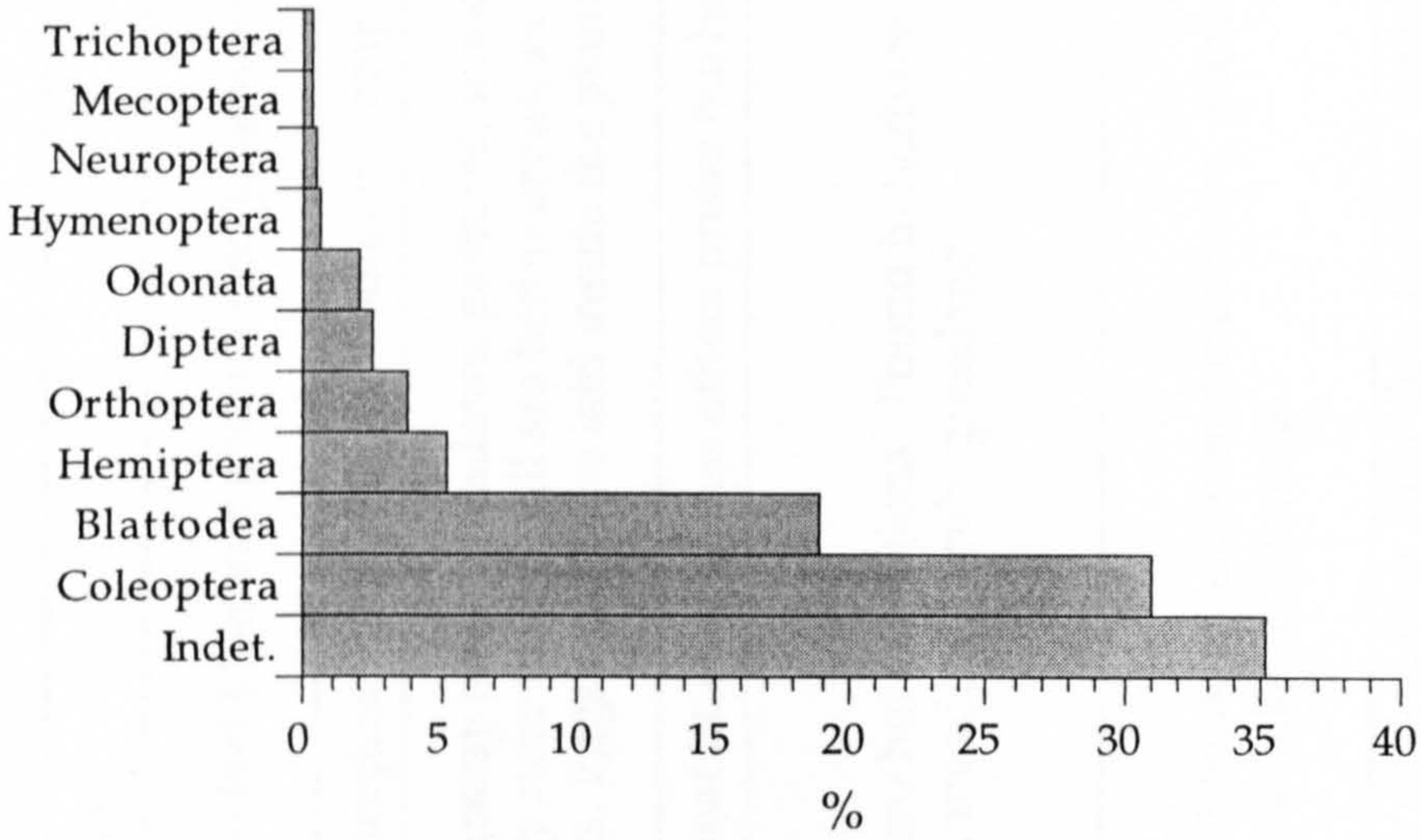


Figure 5.04 Wealden insect fauna. (After Jarzembowski 1991a).

ORDER	FAMILY	COMMON NAME	ECOLOGY
Coleoptera	Cupididae		Common in leaf litter and around decaying wood.
	Elateroidea	click beetles	
Blattodea	*Mesoblattinidae*		Generally tropical/subtropical. Found in damp leaf litter.
Homoptera	Cicadellidae	leafhoppers	Found in grassy areas, meadows, pastures, woodland margins particularly near water. All are herbivorous, sucking liquid food from plants. Eggs tend to be laid inside the plants.
	Fulgoroidea	plant hoppers	
	Palaeontinidae		
Heteroptera	*Progonocimicidae*		? Beneath leaf litter or stones others prefer the herbage layer.
Orthoptera	Acridoidea	short-horn grasshoppers	Prefer warm/hot conditions. Found in herbage/leaf litter of woodland, meadow, scrub, grassland.
	Elcanidae		
	Grylloidea	crickets	
	Hagloidea		
Diptera	Mycetophiloidea	fungus gnats	Prefer moist wooded areas and meadows, often close to standing water such as lakes or streams.
	Rhagionidae	snipe flies	
	Tipuloidea	crane flies	
Odonata	*Aeschnidiidae*		Found near/flying over still/slow flowing water. Habitats typically forested or meadow. Eggs laid under water. Nymphs aquatic.
	Corduliidae	cordulid dragonflies	

ORDER	FAMILY	COMMON NAME	ECOLOGY
Hymenoptera	Gasteruptiidae		Associated with flowers. Often nest in hollow stems and rotten wood
	Sphecidae	sand/digger wasps	
Neuroptera	*Brongniartellidae*		Live in woodland, meadow and low scrub.
	Psychopsidae		
Mecoptera	Orthophlebiidae	scorpionflies	Found on low lying vegetation around woodland margins.
Isoptera	Hodotermitidae	rotten-wood termites	Generally consume rotting wood, which they live in or near.

Table 5.1 Faunal list of insects from the Smokejacks site. Extinct families are *italicised*. In addition, Trichoptera and Coccoidea (Homoptera) have been recovered from other Wealden sites (see Cook & Ross 1996). Data taken from Ross & Cook 1996.

5.4.3 Fossil preservation

5.4.3.1 Material and methods. Uncurated rock fragments of a lens recovered from the Smokejacks Brickworks pit (Ross lens: Fig. 5.03) and held by the Natural History Museum (London) were split and the fossils examined. Some thirty insect specimens were recovered from the slabs, all but ten of which were indeterminate beetle elytra. A cockroach wing fragment was the only other determinable specimen. The remainder were too incomplete to allow identification. The structure of the specimens was examined with the SEM (Appendix A1.1) and their mineralogy determined using microprobe analysis (Appendix A1.2).

5.4.3.2 Results

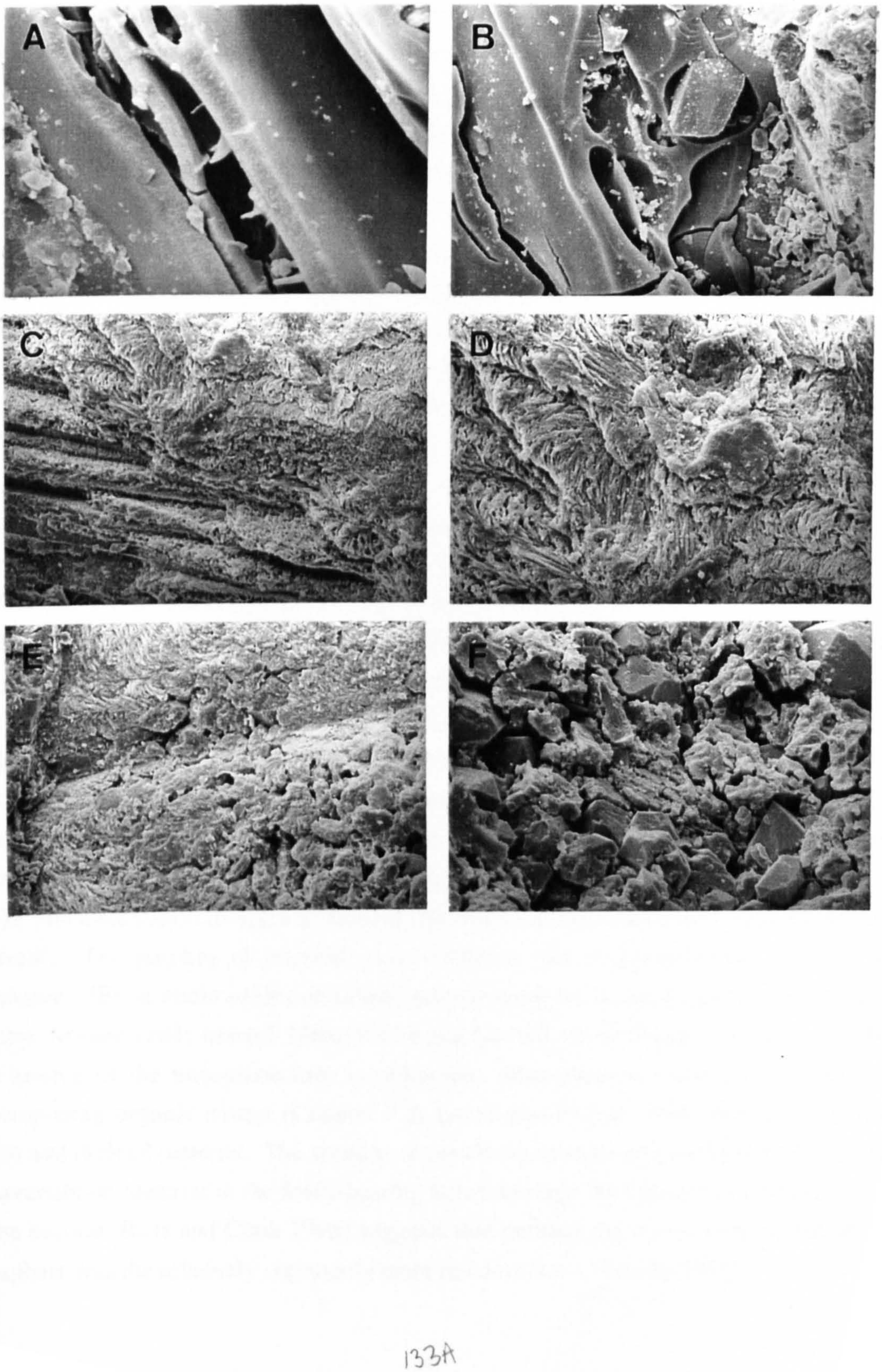
Structural preservation. The majority of specimens retain no original structure. All detail of cuticle is generally destroyed by the growth of a coarse mineral fabric which replicates only the outline of the fossil (Plate 5.1F). The only features recognisable within this coarse fabric are the striations of coleopteran elytra which are preserved as prominent 'ridges' and 'troughs' of crystal.

While the majority of specimens are structureless, a limited number (5) preserve isolated patches of recognizable structure indicative of cuticle morphology. Limited regions of distinctly smooth cuticle (Plate 5.1A, B) (compared to the mineralized material or matrix; Plate 5.1D-F) occur, and suggests organic preservation (see Wilby 1992). Within this material, layers (Plate 5.1A) and canals are evident (Plate 5.1B). However, the limited extent of such material precludes confirmation of the affinity of the structure.

Mineralized cuticle is also evident and confirms the presence of the two-system model of Neville and Luke (1969). Layers with microfibrils arranged helicoidally (Plate 5.1C, D [right hand portion]), and layers with microfibrils arranged in parallel with one preferred orientation (Plate 5.1D [left hand portion]) both occur. An oblique section through the cuticle reveals a crescentic arrangement of microfibrils (commonly observed in the endocuticle of extant insects: Bouligand 1965; Neville 1967; Neville and Luke 1969; Neville *et al.* 1969; Dalingwater *et al.* 1991) (Plate 5.1E). The transformation from mineralized microfibrils to a destructive crystalline fabric may be observed in places (Plate 5.1E).

Mineralogy. The insects of Smokejacks are primarily replicated in calcite, with only occasional small patches of structure organically preserved or replicated in phosphate. The coarse calcite fabric, with laths up to 30μm in length is responsible for only gross replication of structure (*e.g.* striations on coleopteran elytra) (Fig. 5.05). Microprobe analysis revealed that where the structure of the cuticle survives it is preserved in hydroxyapatite (Fig. 5.05). Confirmation of the presence of organic material was not possible by microprobe analysis, and material could not be removed for pyrolysis.

Plate 5.1 SEM images of beetle elytra. A, Organically-preserved layers within the cuticle (SJ1). x2250. B, Canals within the cuticle (SJ1). x1000. C, Layers within the cuticle preserved in apatite, revealing helicoidal (right) and unidirectional (left) arrangement of microfibrils (SJ4). x800. D, Apatite-preserved layers of the procuticle, revealing helicoidal arrangement of microfibrils (SJ4). x1600. E, Oblique section through cuticle (SJ3). Crescentic microfibrils, preserved in apatite (left) are replaced by coarse calcite fabric (bottom right). x800. F, Euhedral calcite rhombs, typical of the general preservation of the Smokejacks insects (SJ1). x1100. All specimens in the personal collection of the author. Material figured in future publications will be accessioned by the Bristol City Museum and Art Gallery.


A
B
C
D
E
F

5.5 DISCUSSION

In the insects of Smokejacks, apatite is responsible for the detailed replication of the cuticle, while calcite, on the other hand, rarely preserves even gross structure. The comparison of the taphonomy of these insects to those recovered from other Wealden pits is uncertain, since the Smokejacks insects are recovered from a phosphatic lens while insects of other sites are known to be recovered from recovered from sideritic lenses and concretions.

The precipitation of apatite/calcite has been likened to a switch (Briggs and Wilby 1996; see Chapter 4). Microbial activity is recognized as the principal control on the switch through its influence on pH (Briggs and Wilby 1996). The pH in turn affects the relative concentration of bicarbonate and phosphate produced as by-products of decay (Berner 1968; Briggs and Kear 1994). Where the initial acidic by-products of microbial metabolism (such as CO_2 and H_2S) escape by diffusion, the pH remains predominantly alkaline, and calcite is precipitated. Under closed, anoxic conditions, a fall in pH favours the precipitation of apatite. Since pH can vary within a single carcass, apatite and calcite may form simultaneously in different parts of the decaying animal (see Briggs and Kear 1993a). The pH may also vary with time such that phosphatized tissue is overgrown by calcite, reflecting a gradual rise in pH following initial decay (Briggs and Kear 1994b). In the Mazon Creek insects, phosphatization was favoured by the closure of the system following the onset of concretion growth. Initial decay resulted in a fall in pH that favoured apatite. However, continued decay drove the pH back up, so precipitating calcite. In this case, no structure was preserved by either mineral.

The insects of Smokejacks are represented primarily by elytra and wings. The chitinous microfibrils are preserved in apatite, while the interstitial proteins are absent, suggesting extensive decay prior to mineralization (see Chapter 2). Apatite is recognized as the most important authigenic mineral in the preservation of soft tissue, often replicating structures at a resolution of microns (see Chapter 7.2). Phosphatization has been shown to occur within weeks (Briggs and Kear 1993b, 1994b; Briggs *et al.* 1993). It has even been claimed that phosphatization could occur over a period as short as a few hours (Martill 1988; Martill and Harper 1990).

For phosphatization to begin at Smokejacks, the conditions must have been anoxic and 'closed'. The patches of organic tissue indicate that phosphatization was not all pervasive. (Even under ideal conditions, phosphatization is recognized as selective or patchy: Müller 1985; Martill 1988; Wilby and Martill 1992; Briggs and Kear 1993b). The source of the phosphate ions is unknown. Phosphate is known to originate in decomposing organic matter (Chapter 7.2; Lucas and Prévôt 1984; Prévôt and Lucas 1986) and skeletal material. The absence of vertebrate remains and the comparative rarity of invertebrate material in the fossil-bearing lens (although the former is noted elsewhere in the section: Ross and Cook 1995) suggests that perhaps the most likely source of the phosphate was the relatively commonly plant remains (see Connolly 1986).

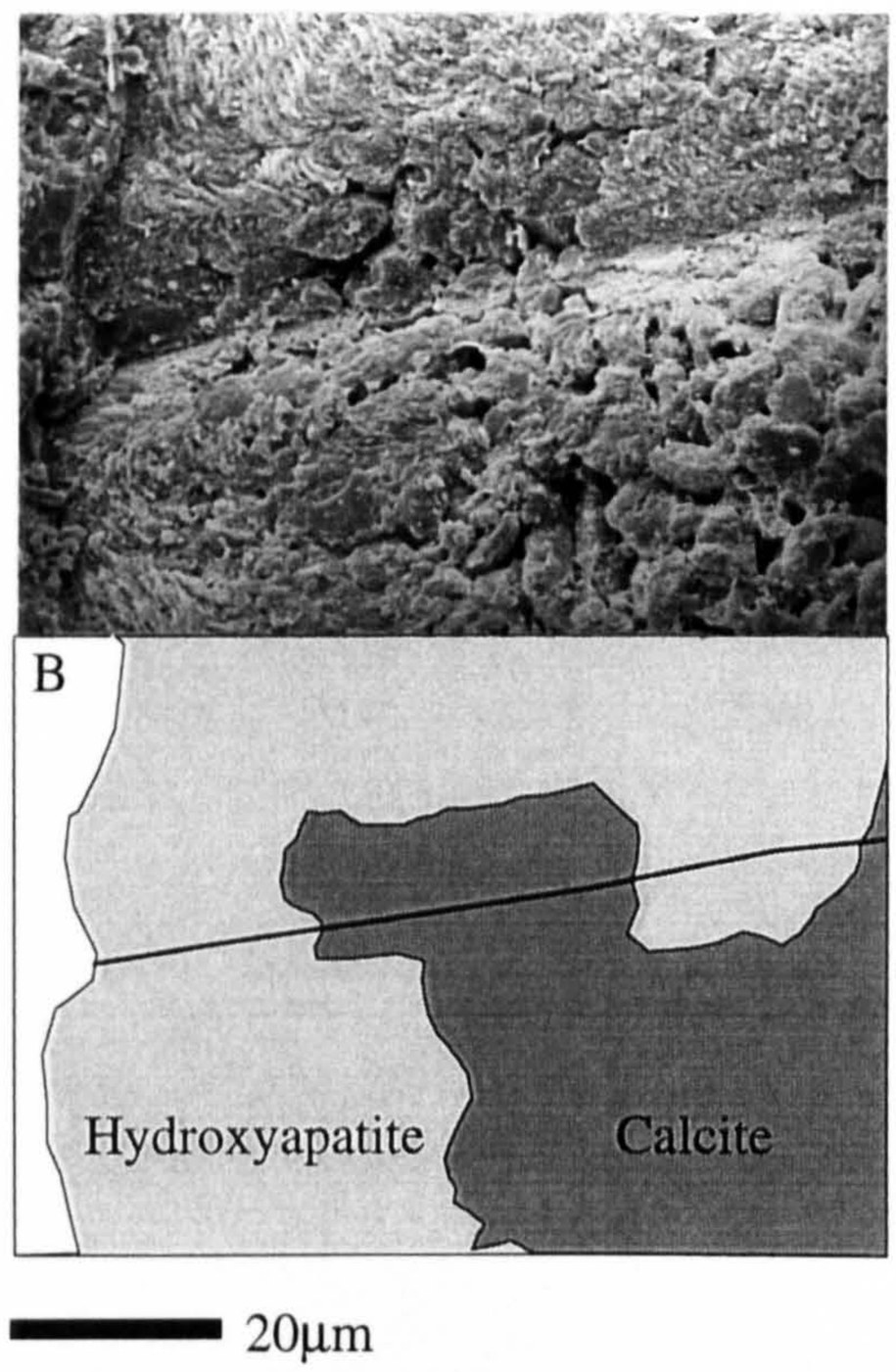


Figure 5.05 A, Photomicrograph of oblique section through beetle cuticle. Crescentic arrangement of microfibrils (left) is destroyed by the coarse crystalline microfabric (bottom right). x. B, Schematic representation of electron microprobe results, based upon selective sampling of points across the surface. Comparison of the two images reveals that apatite is responsible for the preservation of the microfibrils. The coarse crystals are calcite.

Calcification may have occurred simultaneously with phosphatization in different parts of the same carcass (see Briggs and Kear 1993b). However, change from detailed replication in apatite to precipitation of coarse crystalline calcite in certain areas (Plate 5.1E), suggests that following phosphatization the 'switch' was flicked to calcification. The calcite crystals are too large to replicate the delicate structure of the cuticle. A similar phenomenon was noted in the experiments of Briggs and Kear (1994).

CHAPTER 6

GREEN RIVER

6.1 INTRODUCTION

6.1.1 North American Palaeogene lakes

The Palaeogene insect deposits of North America are found in a broad band that stretches from British Columbia to Colorado (Wilson 1978; Lewis and Heikes 1993; Fig. 6.01, to which *locality numbers* in italics below refer; Table 6.1). The deposits are lacustrine in nature and range from the small, isolated basins of British Columbia (Wilson 1977b; Douglas and Stockey 1996, *28-34*) and Lake Florissant (Gazin 1935; Leopold and MacGinitie 1972, *36*), to significant waterbodies that occupied several basins and thousands of hectares, *e.g.* the Green River Lake complex (Schaeffer and Mangus 1965; McGrew and Casilliano 1975; Grande 1989, 1994; Franczyk *et al.* 1992, *13-21*). Throughout the early Tertiary these intermontane lakes waxed and waned, ultimately disappearing by the Neogene.

The Tertiary lake sediments of North America commonly record deep to shallow, near shore environments (see Bradley 1948; McGrew 1975; Eugster and Hardie 1975; Surdam and Wolfbauer 1975; Wilson 1977a, b; Lewis 1989; Franczyk *et al.* 1992), although coal-swamps (Wilson 1978) and playa-lake conditions (Eugster and Surdam 1973) are represented. The sediments are generally fine grained varved shales, suggesting both quiet depositional conditions and a stratified water column (Bradley 1948). The sediments often contain high levels of exploitable kerogen (Cole 1983). The region experienced considerable volcanic activity during sedimentary deposition, as evidenced by frequent horizons of tuff and bombs. Occasionally insects are preserved in these tuffaceous horizons (Copper Basin: Axelrod 1966, *24*; British Columbia: Wilson 1977b; Douglas and Stockey 1996; Republic: Douglas and Stockey 1996, *27*), or in re-worked volcanic dust (Ruby River: Lewis 1971, *37*; Florissant: Leopold and MacGinitie 1972).

The climate of the region during the Palaeogene was temperate to sub tropical and generally humid (Leopold and MacGinitie 1972; see section 6.3.3). Higher altitude localities such as Creede (Cockerell 1941; Wilson 1968; Leopold and MacGinitie 1972; *35*) and Copper Basin (Axelrod 1966) were cooler. The higher latitude deposits also experienced lower temperatures (Rouse *et al.* 1971; Douglas and Stockey 1996). High altitude may be responsible for the low diversity of insect species at some of the localities (Carpenter *et al.* 1938).

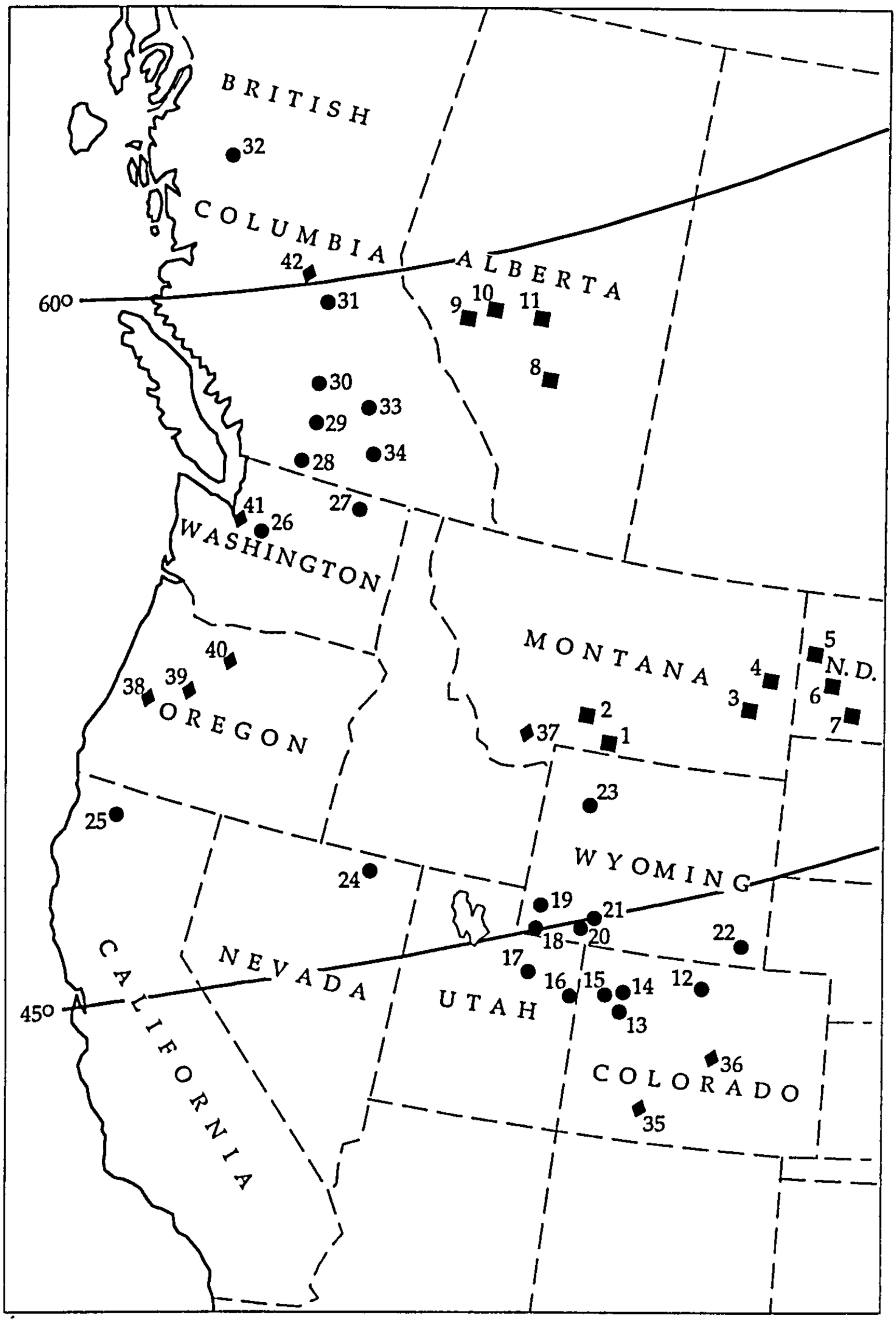


Figure 6.01 Palaeogene insect faunas in western North America. Squares are Palaeocene localities, circles are Eocene, diamonds are Oligocene. The heavy oblique lines are reconstructed Eocene latitudes. Locality numbers refer to Table 6.1. (After Wilson 1978 and Lewis & Heikes 1991).

	Locality		Formation	Insect fauna	Author
1	Bear Creek	MO	Fort Union	Trich, Blatt, Hem, Od	Cooper 1941
2	?	MO	Fort Union	Trichoptera, Blattodea, Odonata	Brown 1957, 1962
3	Cherry Creek	MO	Fort Union	Trichoptera, Blattodea, Odonata	Brown 1957, 1962
4	?	MO	Fort Union	Trichoptera, Blattodea, Odonata	Brown 1957, 1962
5	Sheep Butte	ND	Sentinel Butte	Trichoptera	Erickson 1985
6	Wannagan Creek Quarry, near Medora	ND	Tongue River	Odonata, Trichoptera	Lewis 1988, Melchior & Hall 1983
7	Telephone Tower Hill	ND	Golden Valley	Homoptera, Odonata, Trichoptera	Fennah 1968
8	Red Deer River	Alb	Paskapoo	Odon, Ephem, Hem, Col, Orth, Dip, Blatt, Hym; larvae	Mitchell & Wighton 1979; Kevan & Wighton 1981, 1983; Wighton 1982
9	Robb	Alb	Paskapoo	Trichoptera	Wilson 1977, 1982
10	Edson	Alb	Paskapoo	Trichoptera	Wilson 1977, 1982
11	Sundance	Alb	Paskapoo	Hemiptera	Wilson 1977, 1982

Table 6.1 Palaeogene insect localities of North America. Locality numbers (far left column) refer to Fig. 6.01. Column three, refers to state 'zip code' of each State (see Fig 6.01).

	Locality		Formation	Insect fauna	Author
12	Coalment (Spicer, Big Muddy Pass)	CO	Coalment	Coleoptera	Cockerell 1916, 1918; Rodeck 1938
13	Piceance Ck Basin*	CO	Green River	Mec, Odon, Hem, Col, Trich, Dip, Hym, Orth	Scudder 1893; Cockerell 1924; Pribyl *et al.* 1996
14	Hay Gulch	CO	Green River	Diptera	Cockerell 1916, 1917a
15	Douglas Pass	CO	Green River	Dip, Hym, Col, Hem, Trich, Orth, Thy	Cockerell 1921b; Scudder 1900; Hull 1945
16	White River/ ?Evacuation Ck	UT	Green River	Psoc, Thy, Hem, Col, Lep, Dip, Hym, Mec	Scudder 1900; Carpenter 1955
17	Timber Creek	UT	Green River	Larval traces	Moussa 1968
18	Mountain View	WO	Green River	Hymenoptera	Brown 1934
19	Bear River, Twin Ck	WO	Green River	Hem, Col, Dip,	Scudder 1900; Cockerell 1909a
20	Petrified Fish Cut, near Green River	WO	Green River	Odon, Orth, Hem, Col, Dip, Hym	Scudder 1878, 1890
21	Jack Morrow Ck	WO	Green River	Trich, Odon, Orth, Col	Bradley 1924; Scudder 1878; Brown 1957

* Piceance Creek Basin - includes Roan Plateau (Carpenter 1955), Kimball Creek (James 1932), Bushy Creek Canyon, Parachute Creek, Roan Mountain, Rifle, East Alkali Gulch, Bear Gulch (Cockerell 1909d, 1921d-f, 1923a, 1925a, 1925c, 1933, 1941; Cockerell & LaVeque 1931)

† Douglas Pass - includes Smith's Ranch, Little Duck Creek, and Cathedral Bluffs (Cockerell 1921d, e, 1925a)

	Locality		Formation	Insect fauna	Author
22	Horse Creek	WO	N/A	Trichoptera	Scudder 1890b, 1894b
23	Sheridan Pass, Dubois	WO	Wind River	Lepidoptera	Hickey& Hodges 1975
24	Jarbridge, Copper Basin,	NA	Dead Horse Tuff	Coleoptera, Hymenoptera	Wilson 1978; Axelrod 1966
25	Phillip's Sawmill, Montgomery Ck	CA	N/A	Odonata	Cockerell 1930; Pierce 1944
26	Roslyn, nr Cle Elum	WA	Roslyn	Homoptera, Coleoptera, Diptera	Wilson 1978
27	Republic	WA	Klondike Mountain	Hem, Col, Dip, Eph, Od, Der, Orth, Hym, Iso, Blatt, Neur, Trich, Lep	Wilson 1978; Lewis & Carroll 1991
28	Princeton	B.C.	Allenby	Blat, Hem, Col, Dip, Hym	Wilson 1977
29	Merritt	B.C.	Allenby	Coleoptera	Wilson 1977
30	Tranquille Creek	B.C.	Kamloops Gp.	Diptera, Hymenoptera	Wilson 1977
31	Horsefly	B.C.	Horsefly Beds	Iso, Orth, Meg, Trich, Hym, Dip, Raph	Wilson 1977
32	Smithers, Driftwood Creek	B.C.	Ootsa Lake Gp.	Hem, Dip, Trich, Hym	Wilson 1977
33	Blackburn	B.C.	Allenby	Diptera, Hymenoptera	Rice 1959, 1968
34	Mission Creek	B.C.	Allenby	Diptera, Hymenoptera	Rice 1959, 1968

	Locality		Formation	Insect fauna	Author
35	Creede	CO	Creede	Iso, Neur, Dip, Hym, Od	Carpenter *et al.* 1938 Cockerell 1940; Cuffey *et al.* 1982
36	Florissant	CO	Florissant	Col, Trich, Dip, Hym, Orth, Eph, Embio, Hem, Neur, Iso, Od, Mec, Lep, Coll, Thy, Der	see Lewis & Heikes 1991 for full reference list
37	Ruby River Basin	CO	Passamari	Eph, Od, Orth, Derm, Iso, Plec, Hem, Neur, Col, Trich, Lep, Dip, Hym	Lewis 1988; Lewis & Heikes 1991
38	Goshen	ON	Eugene	Odonata	Fraser 1955
39	Post, Crooked River Basin	ON	Bridge Creek Shales, John Day Series	Od, Col, Dip, Hym	Cockerell 1927; Reyes-Costillo 1977
40	Fossil	ON	Bridge Creek	Trichoptera	Lewis & Heikers 1991
41	Canton Creek, nr Enumclaw	WA	Nachez	Trichoptera	Lewis & Heikers 1991
42	Quesnel, Fraser River Valley	B.C.	N/A	Hemiptera, Coleoptera	Scudder 1890a,1895b; Handlirsch 1910
43	Badlands National Park	S.D.	Brule	Coleoptera, Hymenoptera	Retallack 1984

6.1.1.1 General insect taphonomy. The Palaeogene insects appear remarkably well preserved in hand specimen. However, scanning electron microscopy of specimens from the Ruby River, Creede, Florissant and the Piceance Creek Basin (see section 6.7.3.1) reveals little detail, except the basic body outline. The fossils generally consist of structureless organic material (Plate 6.6A-B).

Insect-bearing deposits of the American Palaoegene can be divided into two major categories based on preservation: deposits where only more decay resistant fragments such as wings, elytra and trichopteran larval cases, are preserved, *e.g.* Copper Basin (Wilson 1978), Red Deer (Wighton 1982; *8*), Coalment (Cockerell 1918; Wilson 1978; *12*), and Montana (Cooper 1941; Brown 1957, 1962; *1-4*); and deposits which preserve a high diversity of more or less intact insects.

Where intact specimens preponderate, the deposits are dominated by Coleoptera (Green River: Scudder 1890b; Cockerell 1917, 1921d, e, f; Pribyl *et al.* 1996; Ruby River: Becker 1960; Lewis *et al.* 1990; Lewis 1991), Diptera, particularly Bibionidae and Tipulidae (Republic: Lewis 1992; British Columbia: Wilson 1977a, b), or Hemiptera, particularly Gerridae (British Columbia: Wilson 1977a, b; Lewis 1989; Archibald 1995). Hymenoptera (Formicidae and Ichneumonidae) are also common, but with the exception of Florissant (Lewis 1991), rarely dominate the fauna. Neuroptera dominate only the Creede biota (Carpenter *et al.* 1938). A complete insect faunal list for the North American Palaeogene lakes is included as Appendix A3.1.

The non-insect biota includes tetrapods (including frogs and other amphibians, lizards, alligators and crocodiles, and mammals: Grande 1984, 1994), birds (including complete specimens and feathers: Grande 1994), fish (Cope 1870; Buchheim and Surdam 1977; Grande 1984, 1989, 1994), and molluscs (LaRocque 1956; Grande 1984, 1994), as well as other arthropods, such as spiders (Dayvault *et al.* 1995), scorpions (Perry 1995) and decapods (crayfish and shrimps: Feldmann *et al.* 1981). Plant fossils such as leaves, roots, branches, seeds, and even flowers are abundant (Axelrod 1966; MacGinitie 1969).

6.2 GREEN RIVER LAKE SYSTEM

6.2.1 Introduction

A number of intermontane basins that formed during the Laramide orogeny (end Cretaceous - Eocene) (Tweto 1975; Norris *et al* 1996) were slowly filled by the run-off from the surrounding tectonic highlands. These freshwater lakes supported a varied and abundant fauna. The Green River lake system (early Palaeocene - end Eocene) was composed of three lakes: Fossil Lake, Lake Gosuite and Lake Uinta (Franczyk *et al.* 1989, 1992) (Fig. 6.04).

Fossil Lake was the deepest of the three but the smallest in surface area (Grande 1984; Grande and Buchheim 1994). During a relatively short history, the lake expanded and contracted several times (McGrew and Casilliano 1975) and may have united with the

larger Lake Gosuite to the east (Grande 1984). The majority of the Green River fossil fish are collected from the sediments of Fossil Lake (Grande 1984, 1989; Grande and Buchheim 1994). Abundant plants, insects and molluscs are also recovered.

Lake Gosuite was a shallow, playa-lake complex for much of its history (Eugster and Surdham 1973; Surdham and Wolfbauer 1975), but may have been deeper in some regions (Boyer 1982). The lake became eutrophic during several periods, supporting algal mats over much of the bottom (Grande 1984). This eutrophic state was responsible for reductions of both diversity and average fish size compared with those of Fossil Lake (Grande 1984). Several plant/insect beds are intercalated between beds of small fish, suggesting emergence and re-flooding.

Lake Uinta was the longest lived of the Green River lakes. Although typically lagoonal to shallow lacustrine for much of its history, the sequence includes many deltaic horizons (Baer 1969). Vast quantities of high grade oil shale are estimated (~290 billion barrels of oil: Cole 1983). At maximum stand the lake occupied both the Uinta and Piceance Creek Basins (Franczyk *et al.* 1992) (Fig. 6.04). Insects and plants are the most common macrofossils (Stokes 1978; Parker 1970; MacGinitie 1969; Pribyl *et al.* 1996); little has been published on the fish fauna (Grande 1984).

6.2.2 Aims and scope of work

Although many publications record the entomofauna of the Green River, and many papers discuss the stratigraphy of the oil-rich horizons of the region, there are none that detail the relationship between lithology, taphonomy and insect diversity, bed by bed, through the sequence. The classic Green River sites have been heavily exploited. In 1990, over thirty full time quarrymen were employed to extract the fossils of the Fossil Butte Member alone (Grande 1994). A number of field guides have been published (*e.g.* Graham 1993a, b) revealing the location of the most fossiliferous localities, and field excursions and collecting trips have taken their toll.

The discovery of four new sites in the Piceance Creek Basin area in 1991-1993 (Anvil Points, Paleoburn, Mahaffey Trail and Old Mountain; Fig. 6.04) and a fifth in 1996 (Denson; Fig. 6.04) afforded an opportunity both to recover specimens and to document fully the stratigraphy of sites that have not thus far been exploited by reckless collectors. By 1996 the sites had produced nearly 50,000 individual specimens on 15,000 slabs of rock (D. Kohls, *pers. comm.*). Preliminary identification of these insects was conducted by Conrad C. Labandeira and Louis J. Pribyl of the Smithsonian Institution, Washington D.C. (Pribyl *et al.* 1996).

Fieldwork was conducted in the Green River Formation of the Piceance Creek basin of Colorado during the summer of 1996. The lithology, taphonomy and insect diversity of the various sites was logged and documented to provide a clearer picture of the depositional conditions of the Piceance Creek basin. Each outcrop tended to extend laterally no more than 3m. Insect material was collected systematically from the cliff face,

beginning with the lowest beds and working up section. Often particular horizons would prove more fossiliferous and these were followed laterally and exploited. Slabs could be extracted with relative ease from the weathered cliff, and each tended to split along the fossiliferous bedding planes. Such material was extracted from the cliff until indurated, unweathered rock was reached, generally to a depth of no more than 10cm. All specimens were gathered regardless of completeness. In total, some 300 specimens were collected.

The Smithsonian Institution houses a significant collection of material recovered from the Piceance Creek basin localities. Since preliminary specimen identification has been completed, discussion of the fauna is based primarily upon this collection

6.3 GEOLOGICAL SETTING

6.3.1 Introduction

The Green River Formation of the south west Piceance Creek Basin is divided into three members: from oldest to youngest, Douglas Creek, Garden Gulch and Parachute Creek (Cashion and Donnell 1974) (Fig. 6.02). Of the three, the Parachute Creek Member has received the most attention due to its significant oil and mineral deposits (kerogen, nahcolite, dawsonite and halite: Cole 1983). It also contains the most important insect deposits of the Green River Formation.

6.3.2 Oil shale

6.3.2.1 Introduction. The oil shale of the Green River Formation is the greatest known potential oil resource in the world, and the richest and thickest deposits occur within the Piceance Creek basin (Donnell 1961). The Green River 'oil shale' is not strictly a shale but is a magnesian marlstone rich in organic matter (Bradley 1931). However, the term 'oil shale' continues to be employed, and is used here.

The appearance of the oil shale is dependent upon the organic content. Oil-poor shales weather light grey/brown but are distinctively banded with a darker hue. The richer beds weather dark bluish-grey to almost black. Some of the richest beds weather to look like antique unfinished mahogany (Bradley 1931). Fresh surfaces of oil-poor shales are faint brown in hue, while oil-rich are either very dark grey or black with a 'satiny' lustre. The oil shale is composed of pairs of thin laminae termed varves (Bradley 1929). One of the pair is rich in organic material, the other has a high mineral content. The two layers are sharply defined in moderately rich oil shale but are difficult to discern in rich beds. Rich oil shale beds resist erosion and weather to form 'ledges' at outcrop. Barren shale weathers to form slopes (or grooves) (Donnell 1961).

The most economically important oil shale sequence of the Green River is the Mahogany zone of the Parachute Creek Member, deposited during the maximum stand of Lake Uinta (see below). The member is subdivided into 'oil-shale zones', defined by the relative richness or 'leanness' of oil (Cashion and Donnell 1972). The most important is

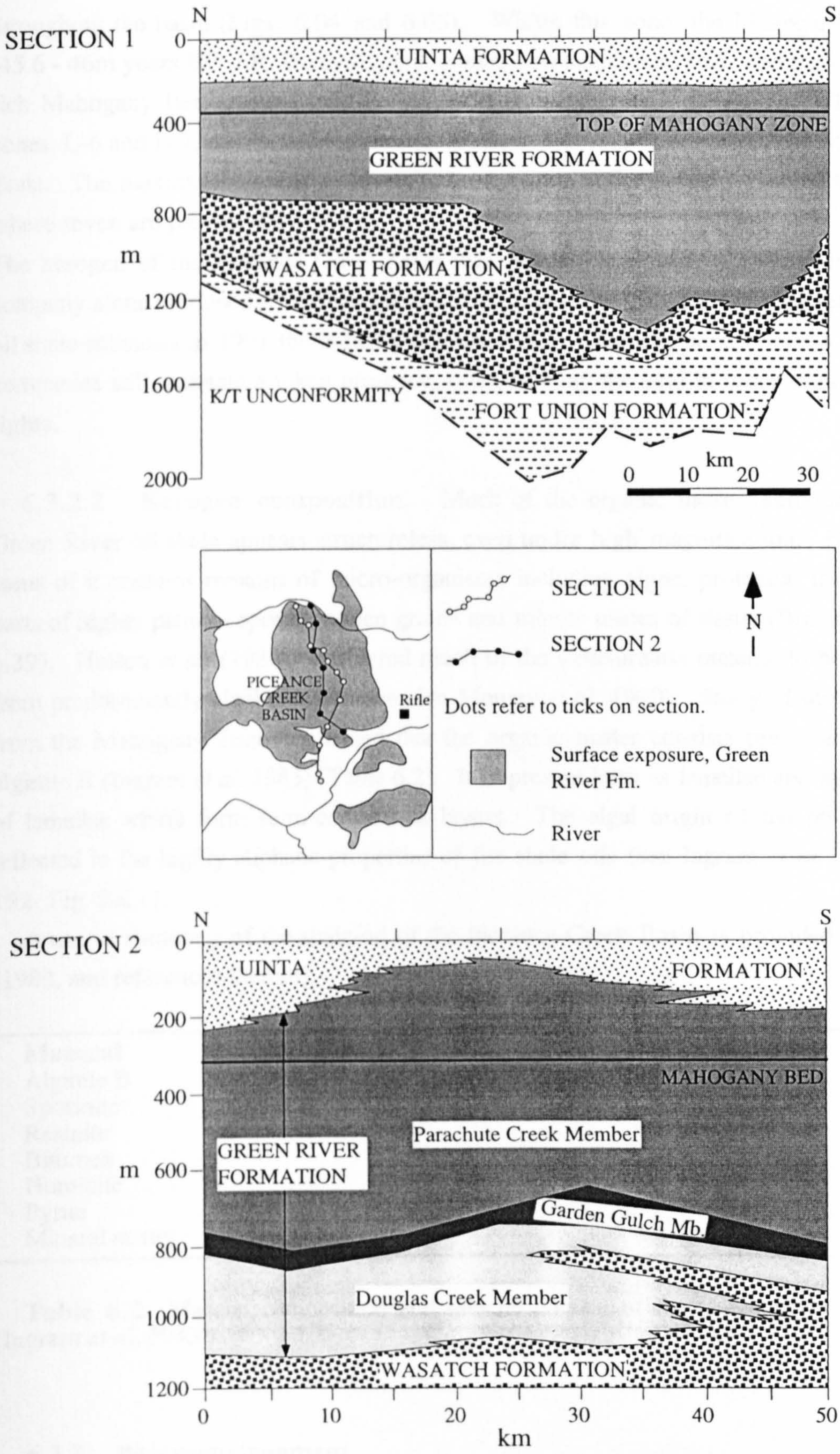


Figure 6.02 Stratigraphic cross sections of the Piceance Creek basin showing depositional lithofacies and stratigraphy. (After Cole 1983).

the R-7 (Mahogany) oil shale zone (or 'ledge' at outcrop) which is readily traceable throughout the basin (Figs. 6.04 and 6.05). Within this zone, the Mahogany Marker (45.6 - 46m years BP: J.R. Donnell, *pers. comm.*), an analcitized tuff, and the dark, oil-rich Mahogany Bed are of particular stratigraphic value (see Fig. 6.05). The 'lean' zones, L-6 and L-7, commonly referred to as the B and A grooves, flank the Mahogany Zone. The maximum number of oil rich zones occurs in the northern part of the basin where seven are present (Cole 1983).

The kerogen of the Piceance Creek basin was heavily exploited, *e.g.* the Unocal oil company alone produced ~5 million barrels of oil a year. However, with the removal of oil shale subsidies in 1991 the industry collapsed (J.R. Donnell, *pers. comm.*). The oil companies still maintain a token presence, often farming the land in order to hold water rights.

6.3.2.2 Kerogen composition. Much of the organic matter (kerogen) of the Green River oil shale appears structureless, even under high magnification. However, some of it contains remains of micro-organisms including algae, protozoa, insects and parts of higher plants - spores, pollen grains and minute pieces of tissue (Bradley 1931, p.39). Hutton *et al.* (1980) considered much of the structureless material to be derived from predominantly algal sources (see also Mourey *et al.* 1980). Study of the oil shale from the Mahogany Zone confirmed that the organic matter consists predominantly of alginite B (Ingram *et al.* 1983) (Table 6.2). It is present both as lamellae and aggregates of lamellae which form semi-continuous layers. The algal origin of the oil shale is reflected in the highly aliphatic properties of the shale oils (see Ingram *et al.* 1983, p. 192, Fig. 2a, c).

A useful summary of the shale-oil of the Piceance Creek Basin is provided by Cole (1983, and references therein).

Maceral	% by volume
Alginite B	44
Sporinite	<0.5
Resinite	<0.1
Bitumen	5
Huminite	2
Pyrite	1
Mineral matter	49

Table 6.2 Maceral composition and mineral content of the Green River oil shale (Ingram *et al.* 1983).

6.3.3 Palaeoenvironment

6.3.3.1 Lake Uinta. By the middle Palaeocene, the Uinta and Piceance Creek basins began to acquire their present day configuration (Franczyk *et al.* 1992; Fig. 6.03).

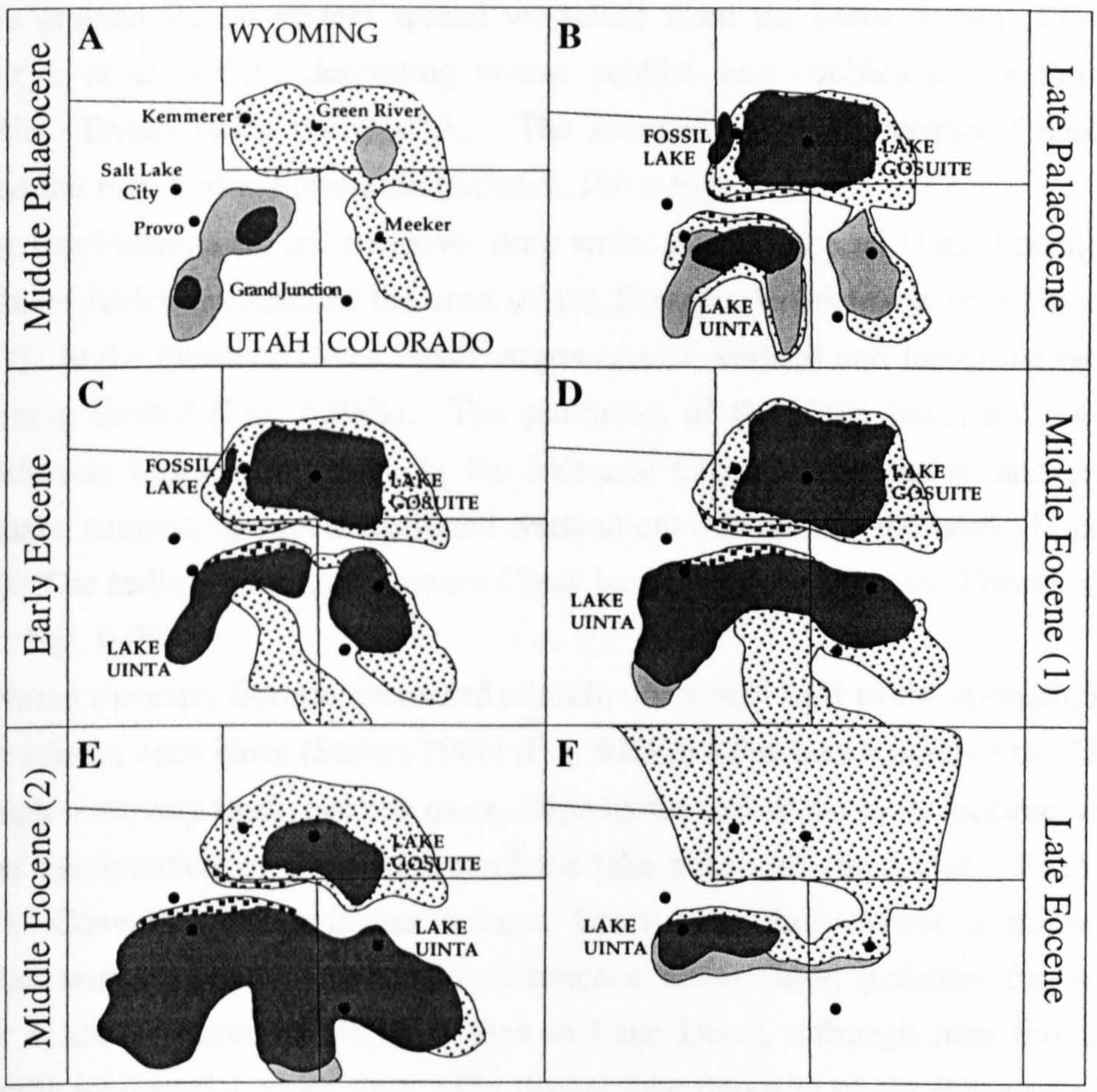


Figure 6.03 Evolution of the Green River Lake System. (Based upon the studies of Franczyk *et al.* 1992).

In the Uinta basin, fan-glomerates from the mountains of the north and west prograded eastward toward the mixed wetland and small isolated lakes of the basin interior (Franczyk *et al.* 1989; Fig. 6.03A). Meanwhile in the northern Piceance Creek basin, a coarse grained fluvial system spread westward from the basin trough (Johnson 1985; Franczyk *et al.* 1992), depositing coarse pebbles and cobbles as conglomeratic lag-deposits (Tweto 1975; Fig. 6.03A). The sediments of the Piceance Creek basin are termed the Fort Union Formation (Donnell 1961; Fig. 6.02).

By the late Palaeocene, an extensive, deep water body occupied Uinta basin, the eastern margin of which approached the crest of the Douglas Creek Arch (see Fig. 6.04; Fig. 6.03B). In the Piceance Creek basin, expansion of wetland and lacustrine environments was more limited (Fig. 6.03B). The sediments of the Uinta basin are predominantly fossiliferous limestones, while in the Piceance Creek basin shales and minor coals dominate, suggesting a more restricted wetland environment in the latter (Franczyk *et al.* 1992). The sediments of the Piceance Creek basin form the Wasatch Formation (Donnell 1961; Fig. 6.02).

During the early Eocene, increased rainfall, ultimately lead to the formation of a large single lake in each basin (Stokes 1986; (Fig. 6.03C). The lake waters of the Uinta basin, although relatively fresh, became more saline by the end of the early Eocene, as indicated by the precipitation of gypsum around the lake perimeter (Ryder *et al.* 1976; Fouch 1981). Coeval sediments in the Piceance Creek basin lack evaporitic minerals. This, together with a characteristic mollusc/ostracode assemblage, indicates that salinity was lower in the Piceance Creek basin than in Lake Uinta, although here too, the salinity gradually increased through time. The deeper lake deposits of the Piceance Creek basin are characterized by widespread, moderately rich oil shale.

By the end of the early Eocene the Uinta and Piceance Creek lakes expanded, breached the Douglas Creek arch and formed the largest of the Palaeogene internally drained hydrologic basins (Bradley 1931; Johnson 1985; Fig. 6.03D), which ultimately covered the entire Uinta and Piceance Creek basins (Fig. 6.03E). The formation of chemical precipitates such as halite (NaCl), nahcolite ($NaHCO_3$) and disseminated dawsonite [$NaAl(OH)_2CO_3$] in the Piceance Creek basin, together with the demise of the mollusc population, suggests the absence of a lake outlet, and a consequent rise in salinity/alkalinity (Franczyk *et al.* 1992). At this time, the rich Mahogany Zone oil shale was deposited (Donnell 1961; Franczyk *et al.* 1989, 1992) (Fig. 6.05). The insect-bearing localities discussed below were deposited during this period of maximum stand. The sediments of both lakes comprise the important insect-bearing Green River Formation (Donnell 1961; Fig 6.02).

Subsequently, the lake decreased in size as a deltaic wedge and major volcaniclastic influx prograded southwards from Wyoming. By the late Eocene, the lake had shrunk to the western and north-central part of the Uinta basin (Fig. 6.03f). Lake salinity was high, as evidenced by abundant bedded evaporites (Dyni *et al.* 1985). These sediments

constitute the Uinta Formation (Surdam and Stanley 1979, 1980; Johnson 1985; Fig 6.02). During the latest Eocene (37.6Ma) the Green River lake system disappeared (Bryant *et al.* 1989), mantled by extensive volcanic and volcaniclastic deposits (Witkind and Marvin 1989; Bryant *et al.* 1989).

6.3.4 Palaeoclimate

The flora and fauna of the Green River Formation indicate a tropical to sub-tropical climate. Abundant palm fronds, balloon vines, lily pads and other tropical/subtropical plants are present (MacGinitie 1969; Herendeen *et al.* 1990). Large reptiles such as crocodiles, alligators, lizards, boa constrictors and neotropical wood snakes were also common (McDowell 1987; Grande 1994; Dayvault *et al.* 1995). A number of tropical fish families whose extant relatives survive today only in tropical Africa, South America and the Indo-west Pacific are also reported (Grande 1989). The insects, including a number of species of termite, also have a sub-tropical distribution (Scudder 1890; Cockerell 1921f; Codlington 1993; Dayvault *et al.* 1995).

Bradley (1929, 1948) was the first to conclude that the climate in the vicinity of the lakes was comparable to that of the present day Gulf Coast of the U.S.A.. On the basis of the fossil flora of the region, MacGinitie (1964) suggested that the temperature never fell below freezing (average temperature 15 - 21°C), and the annual rainfall was 75-100cm. However, isotopic analysis of the Green River Formation suggests that lake waters were derived from snow melt, presumably from the encircling mountains (Norris *et al.* 1996). The mountains must have been high enough to supply sufficient melt water to the lake. Lapse rate calculations suggest a minimum altitude of >3000 m (Norris *et al.* 1996).

6.4 STRATIGRAPHY

6.4.1 Introduction

The insect-bearing sites of the Piceance Creek basin (Anvil Points, Denson, Paleoburn, Mahaffey Trail and Old Mountain) are geographically distant from one another (Fig. 6.04). Access over the intervening rough terrain is by unimproved mine/farm roads that tend to be concentrated where the oil-rich Mahogany Zone crops out (for economic reasons). Delineating the stratigraphic position of the sites was simplified by a number of prominent marker horizons, notably the Mahogany Zone (or Ledge at outcrop) (see Fig. 6.05). The more recessive 'lean' zones, particularly L-6 (B Groove) and L-7 (A Groove) appear as shelves in the cliff profile and as such are often used by road-builders. Consequently the most interesting beds are often obscured by roads. Scree slopes may also obscure the rock face. The following account of the stratigraphy should be read in conjunction with Fig. 6.05. Reference below to vertical height (*enclosed within brackets*) refer directly to the original logs included as Appendix A2.1.

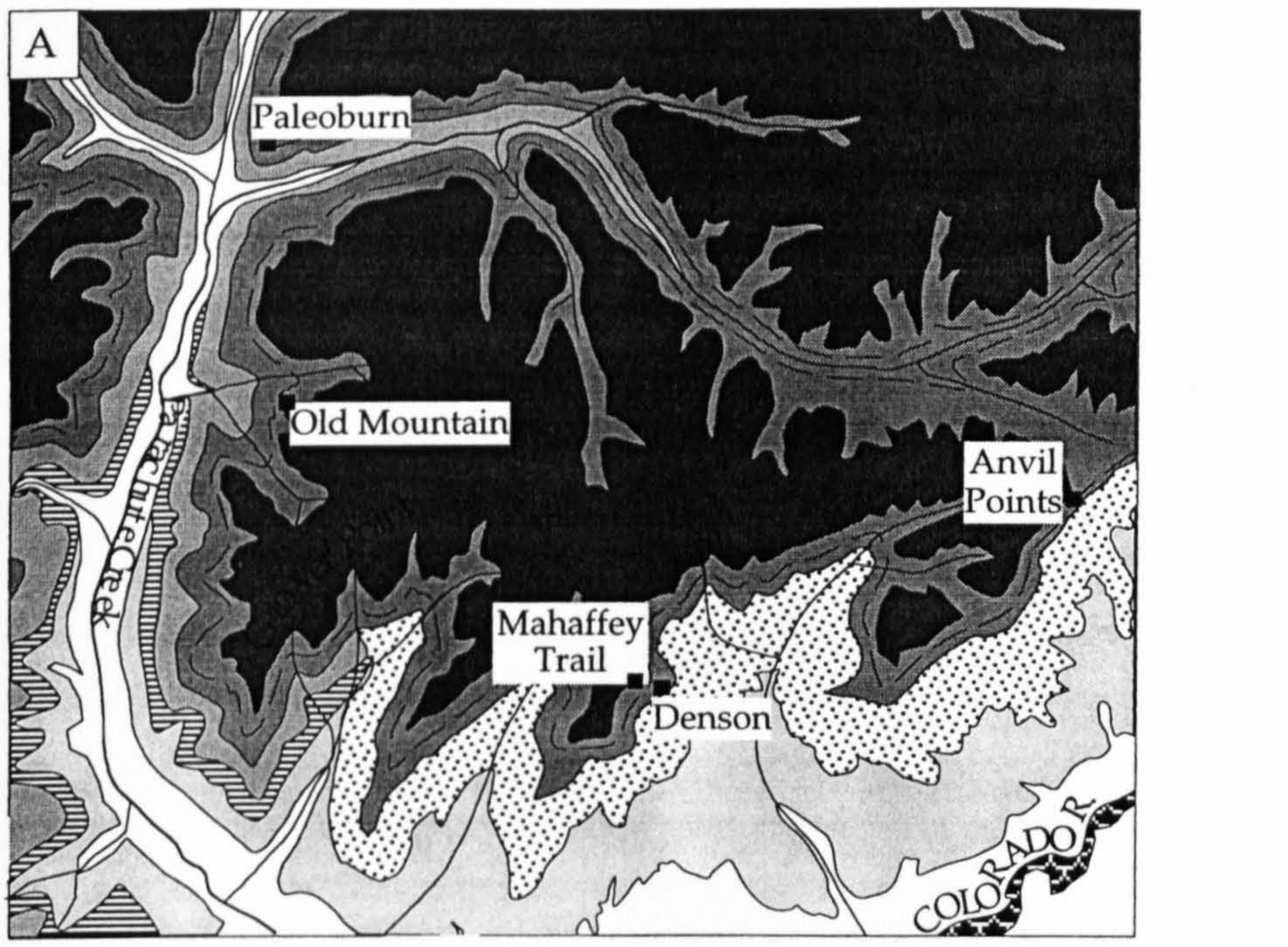


Figure 6.04 A, location of Piceance Creek insect localities. B, outcrop of Green River Formation. (After Hail *et al.* 1989; Grande 1984).

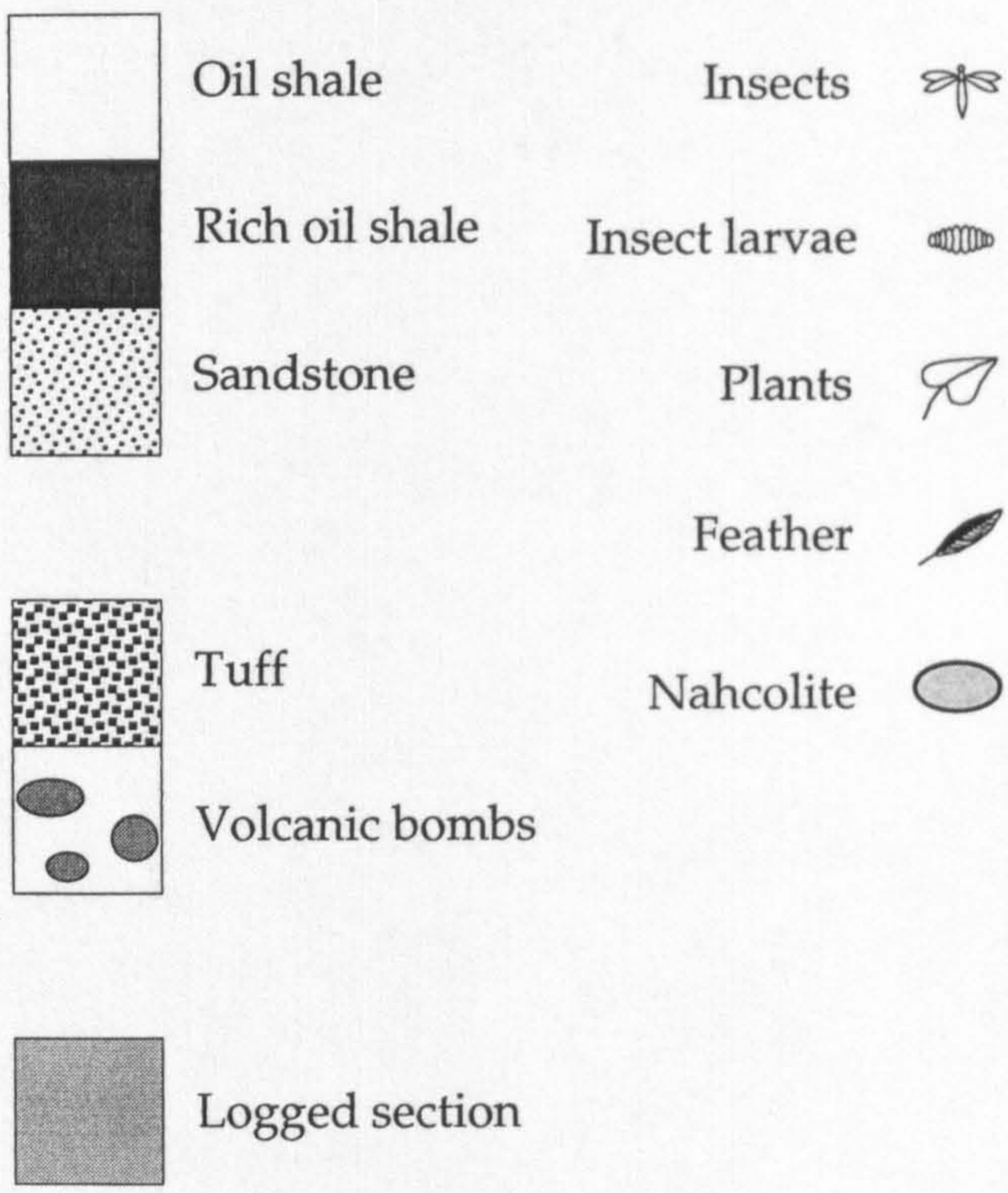
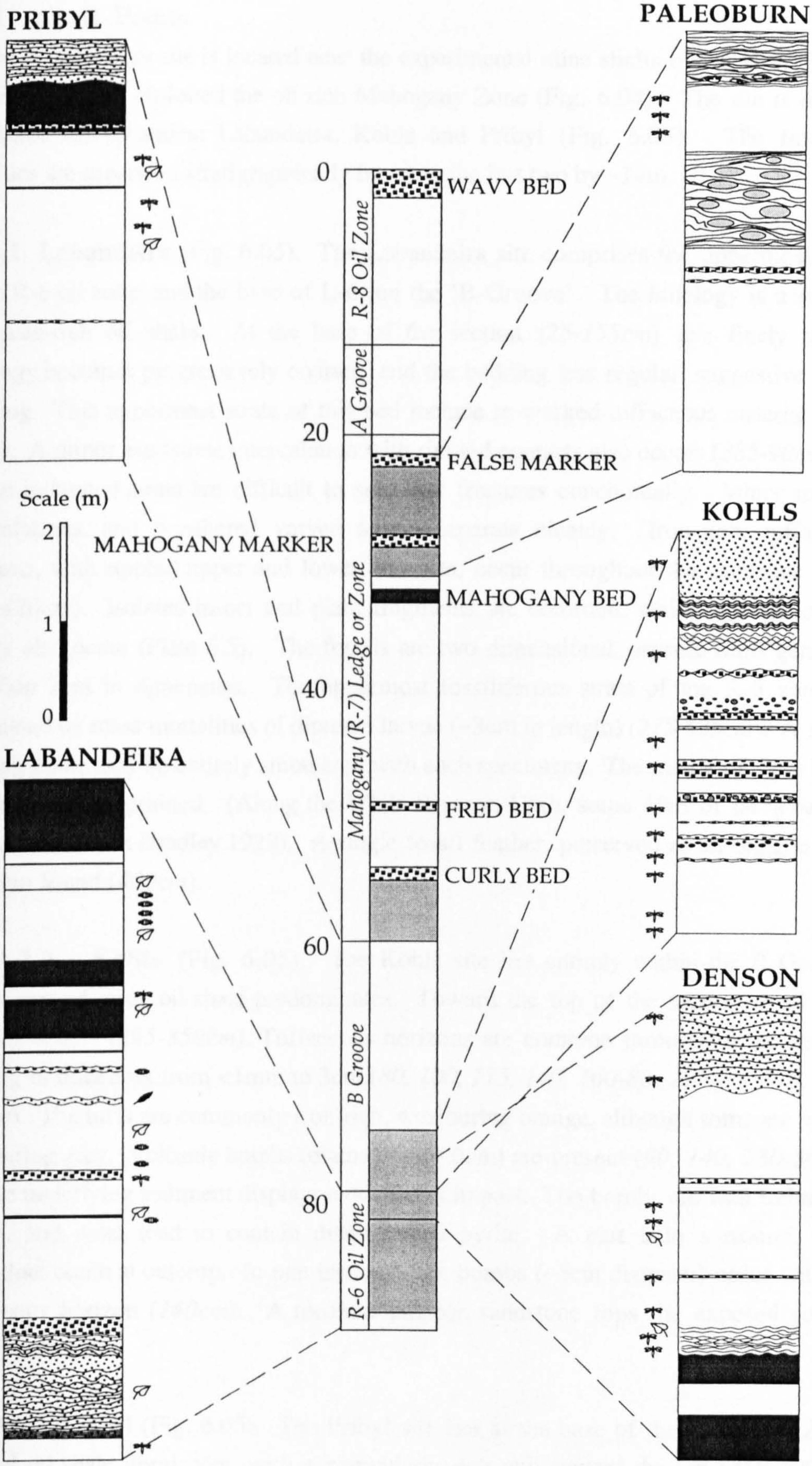


Figure 6.05 Summary logs of the principal insect-bearing sites of the Piceance Creek Basin. The original logs can be found in Appendix A2.1 The central column is adapted from Cashion and Donnell (1972; plot 9). The marker beds occur across the basin.


PRIBYL
PALEOBURN
0
WAVY BED
R-8 Oil Zone
A Groove
20
FALSE MARKER
Scale (m)
2
1
0
MAHOGANY MARKER
KOHLS
MAHOGANY BED
40
Mahogany (R-7) Ledge or Zone
LABANDEIRA
FRED BED
CURLY BED
60
B Groove
DENSON
80
R-6 Oil Zone

6.4.2 Anvil Points

The Anvil Points site is located near the experimental mine shafts of the U.S. Bureau of Mines, which exploited the oil rich Mahogany Zone (Fig. 6.04). The site is divided into three sub-localities; Labandeira, Kohls and Pribyl (Fig. 6.05). The first two localities are separated stratigraphically by ~4m, the last two by ~18m.

6.4.2.1 Labandeira (Fig. 6.05). The Labandeira site comprises the uppermost strata of the R-6 oil zone, and the base of L-6, on the 'B-Groove'. The lithology is a varved, carbonate-rich oil shale. At the base of the section (*25-155cm*) this finely varved lithology becomes progressively coarser, and the bedding less regular, suggestive of re-working. This uppermost strata of this bed include re-worked tuffaceous material (*140-55cm*). A minor sandstone intercalation with rippled contacts also occurs (*385-90cm*).

The indurated strata are difficult to split and fractures conchoidally. Minor micritic intercalations, and weathered varved strata, separate cleanly. Iron-rich, tuffaceous horizons, with rippled upper and lower contacts, occur throughout the sequence (*135, 300, 420cm*). Isolated insect and plant fragments are common, while aggregations of insects also occur (Plate 6.5). The fossils are two dimensional, organic films generally less than 2cm in dimension. The uppermost fossiliferous strata of the R-6 zone are dominated by mass mortalities of dipteran larvae (~3cm in length) (*275-625cm*). A single bedding plane may be entirely smothered with such specimens. The matrix of these larval horizons is finer grained. (Along the White River in Utah, some 60m of larva-bearing beds are recorded: Bradley 1929). A single fossil feather, preserved as an organic film, was also found (*400cm*).

6.4.2.2 Kohls (Fig. 6.05). The Kohls site lies entirely within the B Groove. Finely-varved, grey oil shale predominates. Toward the top of the section small scale rippling occurs (*295-350cm*). Tuffaceous horizons are common throughout the profile, ranging in thickness from <1mm to 3cm (*80, 100, 115, 140, 160-80, 225-80, 310, 350, 365cm*). The tuffs are commonly iron-rich, weathering orange, although some are white, weathering grey. Volcanic bombs (diameter <1 - 6cm) are present (*90, 140, 230-50cm*), and the underlying sediment displays evidence of impact. The bombs are well indurated, heavy, and most tend to contain disseminated pyrite. A rust halo surrounds each individual bomb at outcrop. In one instance, the bombs (~5cm diameter) occur within a tuffaceous horizon (*140cm*). A medium laminar sandstone tops the exposed section (*355cm→*).

6.4.2.3 Pribyl (Fig. 6.05). The Pribyl site lies at the base of the Mahogany Zone. Typical oil shale dominates, with a particularly rich unit toward the top (*350-400cm*). Only three minor tuffaceous horizons are present (*150, 290, 355cm*). The 'Curly Bed' of

Donnell (1961), an irregularly interbedded tuff and medium grained sandstone, in an important straigraphic marker across the basin (*400-450cm*). Insects and plant fragments are restricted to a zone some 1m thick (*225-325cm*).

6.4.3 Denson (Fig 6.05)

The Denson site is located on the boundary between the lands of the U.S. Bureau of Land Management and those of Mobil Oil (Fig. 6.04). Access is hazardous, necessitating breaking a trail across a massive scree slope. The lowermost oil-rich beds of the Denson section (*0-115cm*) are laterally equivalent to the uppermost beds of the Labandeira section. Oil shale predominates. Typical varving is present in all but a 25cm unit where it is replaced by minor rippling (*110-135cm*). Only three tuffaceous horizons are present (*190, 280, 295cm*). The top of the section consists of an irregularly-bedded medium sandstone lens which can be traced laterally in the cliff face for ~15m (*385cm→*). Complete insect and plant fossils are restricted primarily to a 2m zone, although a few fragmentary specimens occur throughout (*135-300cm*).

6.4.4 Paleoburn (Fig. 6.05)

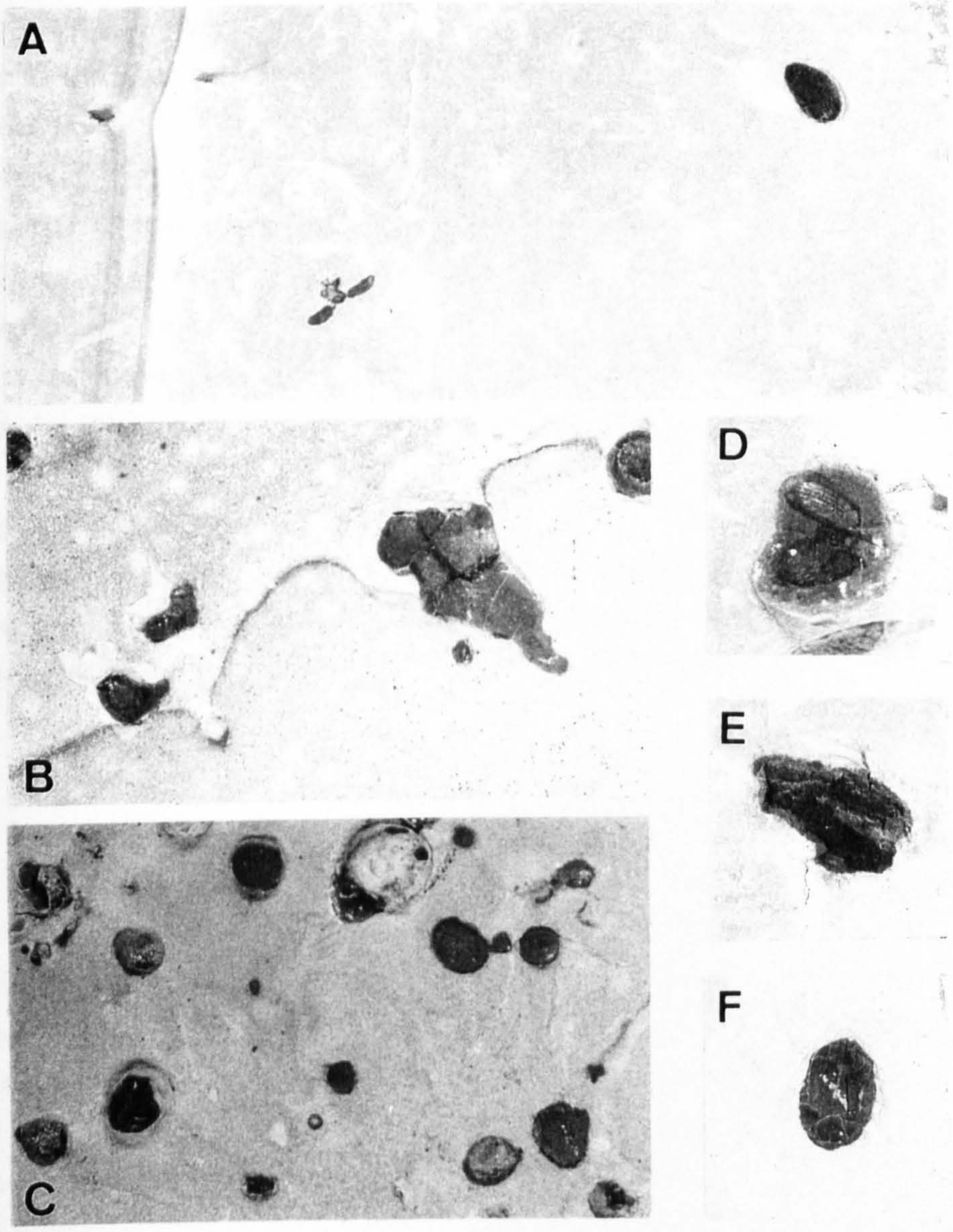
The Paleoburn Site is located on the lands of the Unocal oil company (Fig. 6.04). Stratigraphically, the section straddles the uppermost units of the Mahogany Zone and the A Groove. The outcrop is a striking red pinnacle, proud of the cliff face (Plate 6.1). Similar pinnacles occur across the Middle Fork of the Parachute Creek. Although the sedimentary structures in the Paleoburn sequence are comparable to those at the other sites studied, the rock differs mineralogically (see below). The oil shale has been retorted of kerogen, resulting in a lithology that is less dense than expected and 'rings' when tapped with a hammer. Attempts to trace the lateral extent of alteration were hampered by scree. However the rocks that crop out beyond the scree are similar both structurally and mineralogically to those at the other sites studied, suggesting a maximum extent of some 70m.

Marks suggestive of the passage of water perpendicular to bedding occur throughout the section (Plate 6.2B, C). A number of traces can be observed in detached slabs, where they are evident on the bedding planes, suggesting the passage of a number of 'pulses' (Plate 6.2B, C). Like dark water stains on blotting paper, the traces appear darker (more iron-rich) than the background sediments and often pass through the fossils (Plate 6.2B). Initial attempts to explain the elimination of the kerogen of this site invoked lightening strikes (Dyni 1974). However, no structural evidence to support this hypothesis was found.

A 1m thick horizon including distinctive ellipsoidal vugs (~10-50cm in diameter), from which nahcolite has been leached (J.R. Donnell, *pers. comm.*), occurs (*250-330cm*). The bedding of this zone is greatly distorted by these cavities. Some have fillings of calcite that are evidently the moulds of large radial aggregates of bladed salt crystals (see

Plate 6.1 Paleoburn-type outcrop in Parachute Creek (~height of outcrop 30m). Access prevented inclusion of a similar photograph of the Paleoburn site.

Plate 6.2 Paleoburn concretions. A, Fluid trace (left) affected by small elytral fragment suggests passage of fluid left to right. Beetle, with elytra outspread (centre), and isolated elytra (top right) evident. x0.8. B, Congregation of irregular, barren concretions on the bedding surface. ?Passage of fluid bottom to top. x1. C, Congregation of barren concretions on the bedding surface. x1. D, Concretion nucleated about beetle. Only outspread elytra appear to have survived. x2.2. E, Concretion nucleated about indeterminate insect. x2.5. F, Concretion nucleated about beetle elytron. x2.5. All specimens are currently held in the personal collection of the author.


A
B
C
D
E
F

Bradley 1931). The uppermost bed is the False Marker of Donnell (1961), composed of irregularly interbedded tuff and fine grained sandstone (*415-475cm*), which can be traced across the Piceance Creek basin. The base of the bed contains angular fragments of pumice (~6cm in diameter). The Mahogany Marker tuff (Donnell 1961), also traceable across the basin, is recorded (*220cm*). Only one other minor tuffaceous horizon is evident (*210cm*).

Fossils are restricted to a 60cm zone immediately below the False Marker Bed (*350-410cm*). The fossils are red in colour and surrounded by a halo. Considerably less morphological detail is preserved than at other sites. Toward the base of the fossiliferous unit (*360-375cm*), small (<1cm), red nodules occur, some of which contain insect/plant material (Plate 6.2). However, most nodules are barren.

6.4.5 Old Mountain/ Mahaffey Trail

Fossils were recovered from both these localities, though neither was logged. The sections consist simply of unaltered oil shale. An absence of marker beds made logging impossible in the time available.

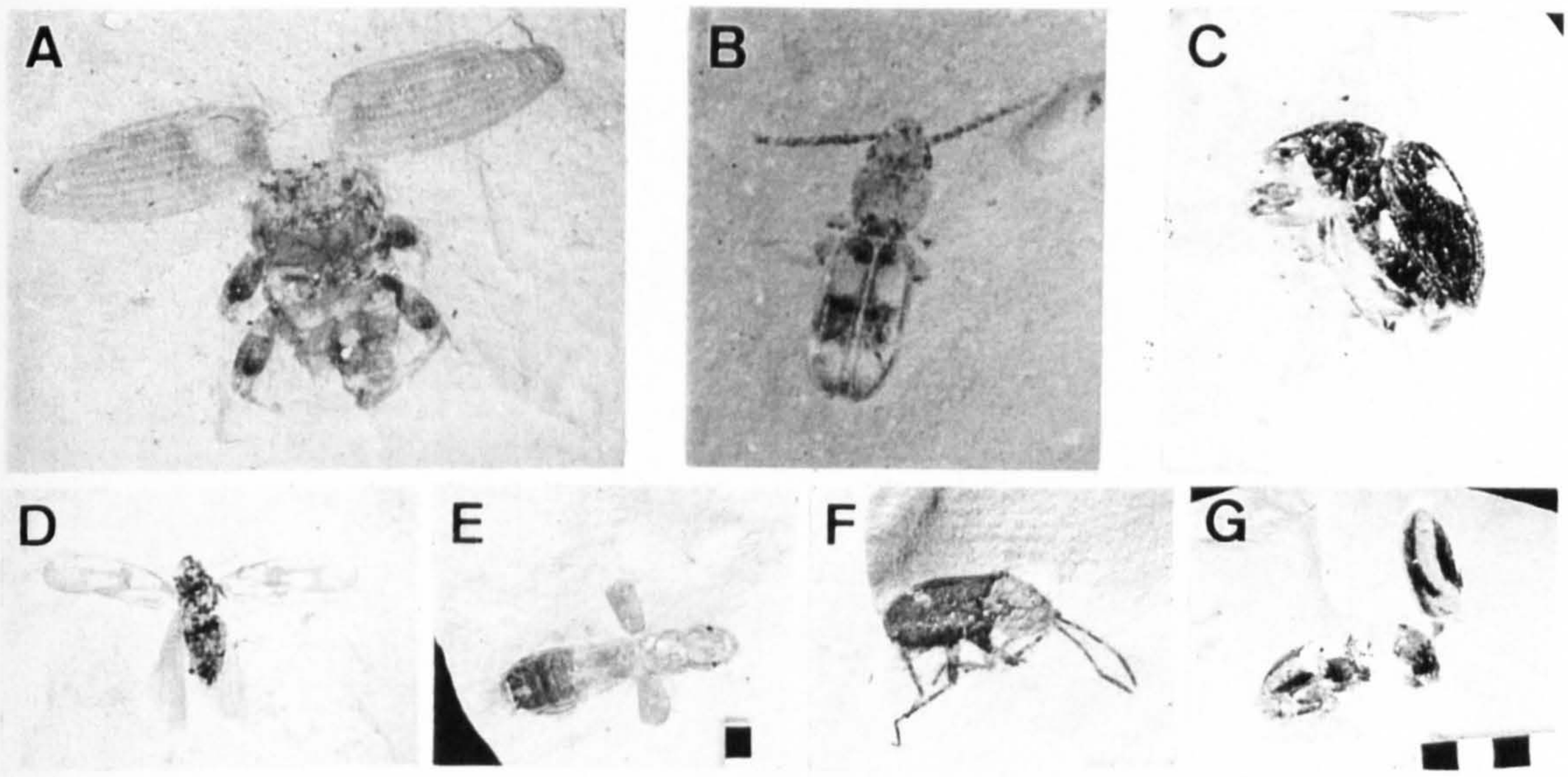
6.5 BIOTA

The relative proportions of the insect orders recovered from the Piceance Creek Basin sites are detailed in Fig. 6.06. The biota is dominated by Diptera (Plate 6.5) and Coleoptera (Plate 6.3), with the orders Heteroptera (6%), Homoptera (6%) and Hymenoptera (5%; Plate 6.4C) of comparable abundance. The fauna of the sites is similar, with the exception of Paleoburn, where Diptera, Hymenoptera and Homoptera are depleted, but Coleoptera and Heteroptera enriched. While the relative proportion of some of the orders recorded may vary slightly as more of the 'insect parts' are identified, the proportions of the more recognizable orders are unlikely to change significantly. The orders Blattodea, Odonata, Orthoptera (Plate 6.4B) and Lepidoptera together account for less than 5% of the fauna. The orders Psocoptera, Colembola, Plecoptera and Rhaphidiodea, Dermaptera and Isoptera are known only from a handful of specimens (Fig 6.06). The percentages are in broad agreement with the findings of Cockerell (1921f), who noted the dominance of Coleoptera, Diptera, Hymenoptera and Homoptera (particularly Fulgoridae) (Cockerell 1917a, 1921f). However, the proportions of taxa collected by Scudder (1890) during a single field season around Douglas Pass (Coleoptera: 63%; Diptera: 22%; Homoptera: 9%; Hymenoptera: 3%) suggest that there is variation across the region. However, since the collecting methods of Scudder are unknown, it is possible that an unquantifiable bias may have been introduced.

A total insect faunal list (including common names) for all the Green River lakes, based upon the catalogues created by Wilson (1978) and Lewis and Heikes (1991) is included as Table 6.3. Recent fieldwork has augmented the published list with

Plate 6.3 Coleoptera of the Piceance Creek basin. A, Ventral surface of unidentified beetle with elytra outstretched. Suggestion of colour banding on legs (APK1). x3. B, ?cerambycid (longhorn) beetle with antennae intact and colour banding of elytra (APL1). x1.6. C, Curculionid (weevil) with distinct rostrum. Legs folded beneath (APL2). x1.6. D, Unidentified bug with elytra outstretched and hindwings intact (APL3). x1.6. E, Staphylinid (rove) beetle with elytra outstretched. Eyes are clearly evident (APL4). x1.5. F, Unidentified beetle with colour banding of legs and antennae (D1). x3. G, Unidentified beetle with colour-banded elytron (D2). x1.8. [APL - Labandeira site; APK - Kohls site; D - Denson].

Plate 6.4 Other orders recovered from the Piceance Creek basin. A, Odonata. Fragmentary wings are the most commonly recovered fossils (D3). x2. B, Orthoptera. Cricket, with both cerci and antennae intact. The antennae had clearly reached a flaccid state before fossilization commenced (APK2). x1.5. C, Hymenoptera. Wasp with colour-banded abdomen (APK3). x1.4. D, Diptera (?Bibionidae). Intact March fly (APL5). x3. E, Diptera (?Culicidae). Intact mosquito on slighter coarser sediment (D4). x3.1. [APL - Labandeira site; APK - Kohls site; D - Denson].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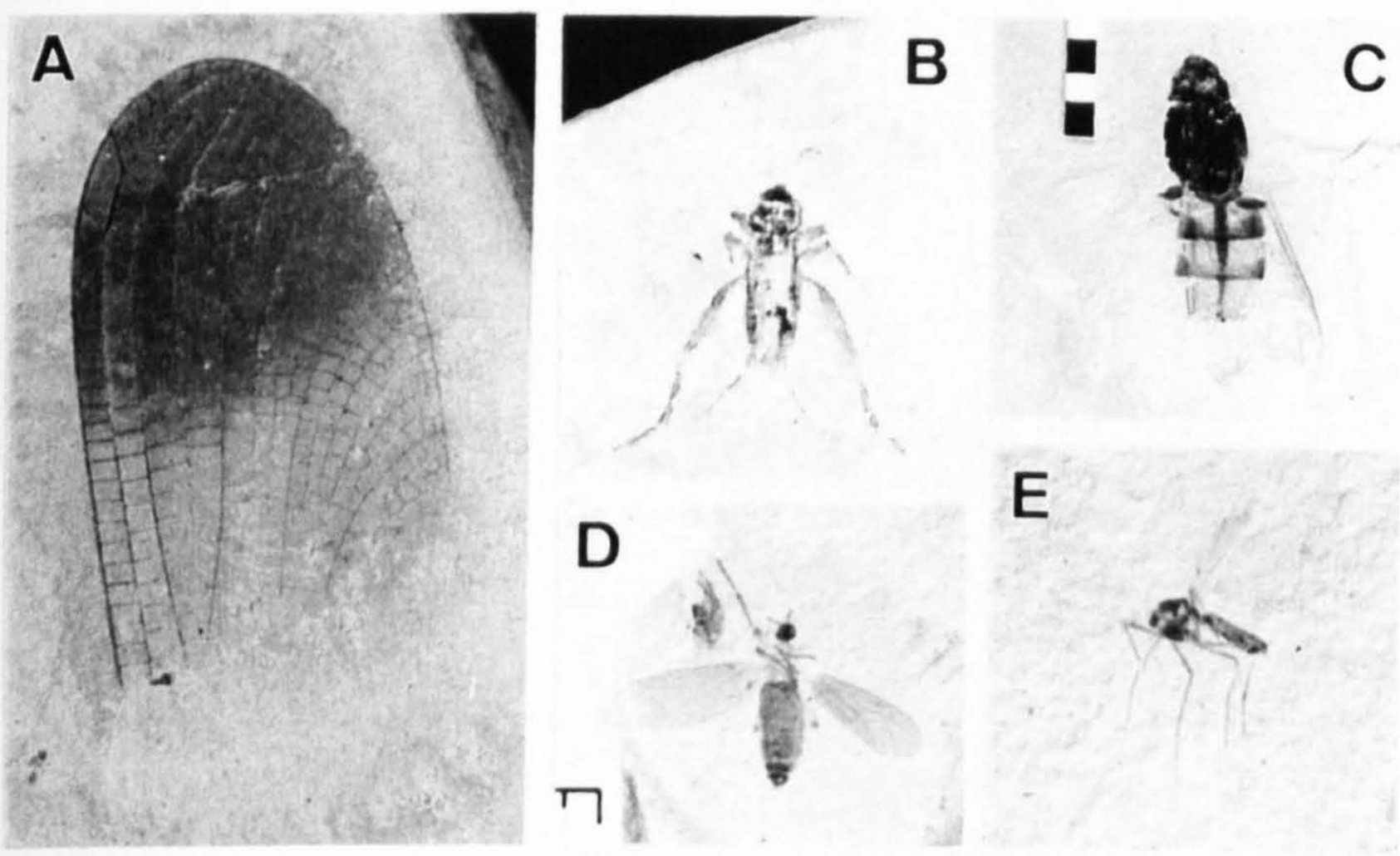
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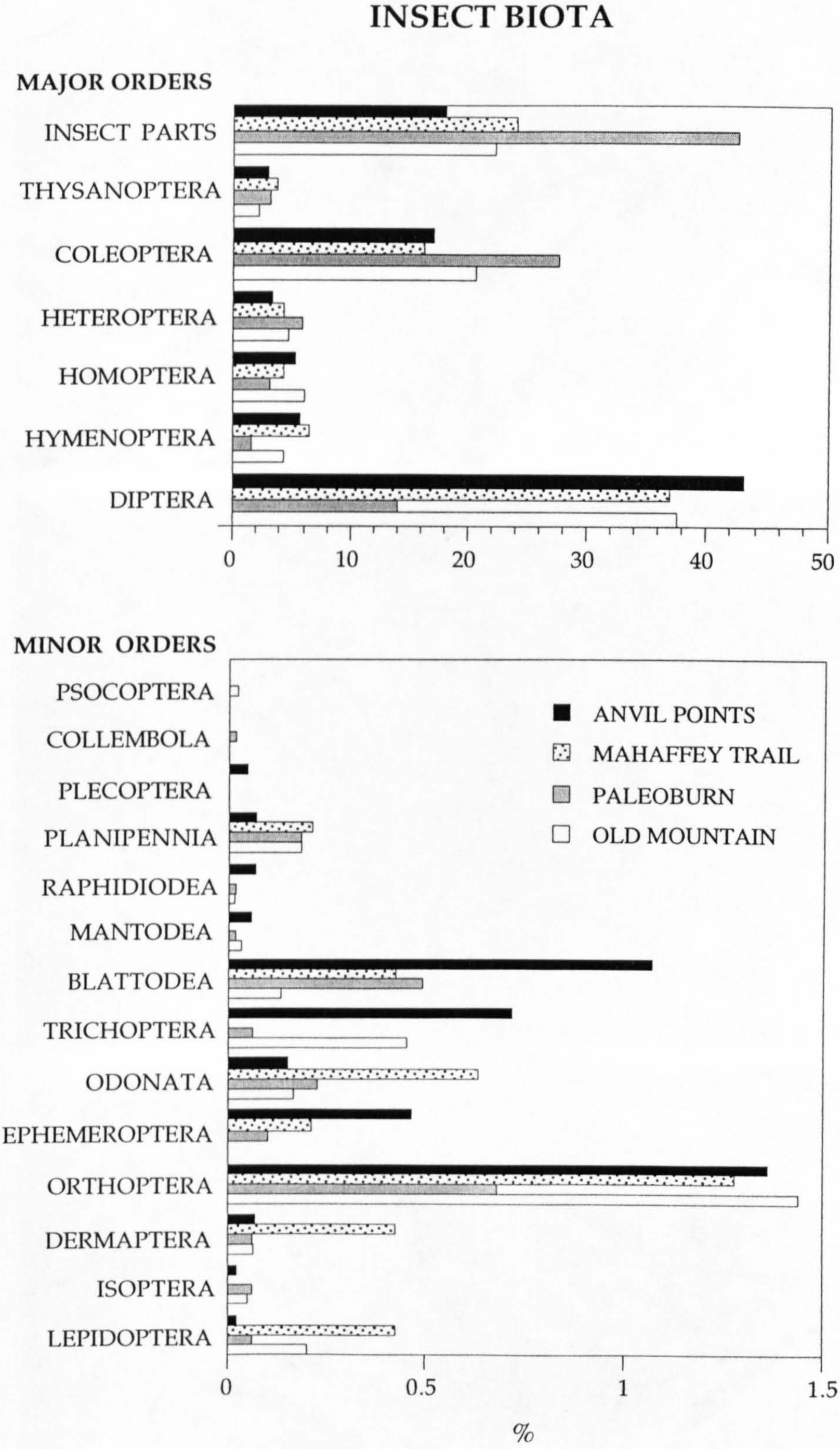
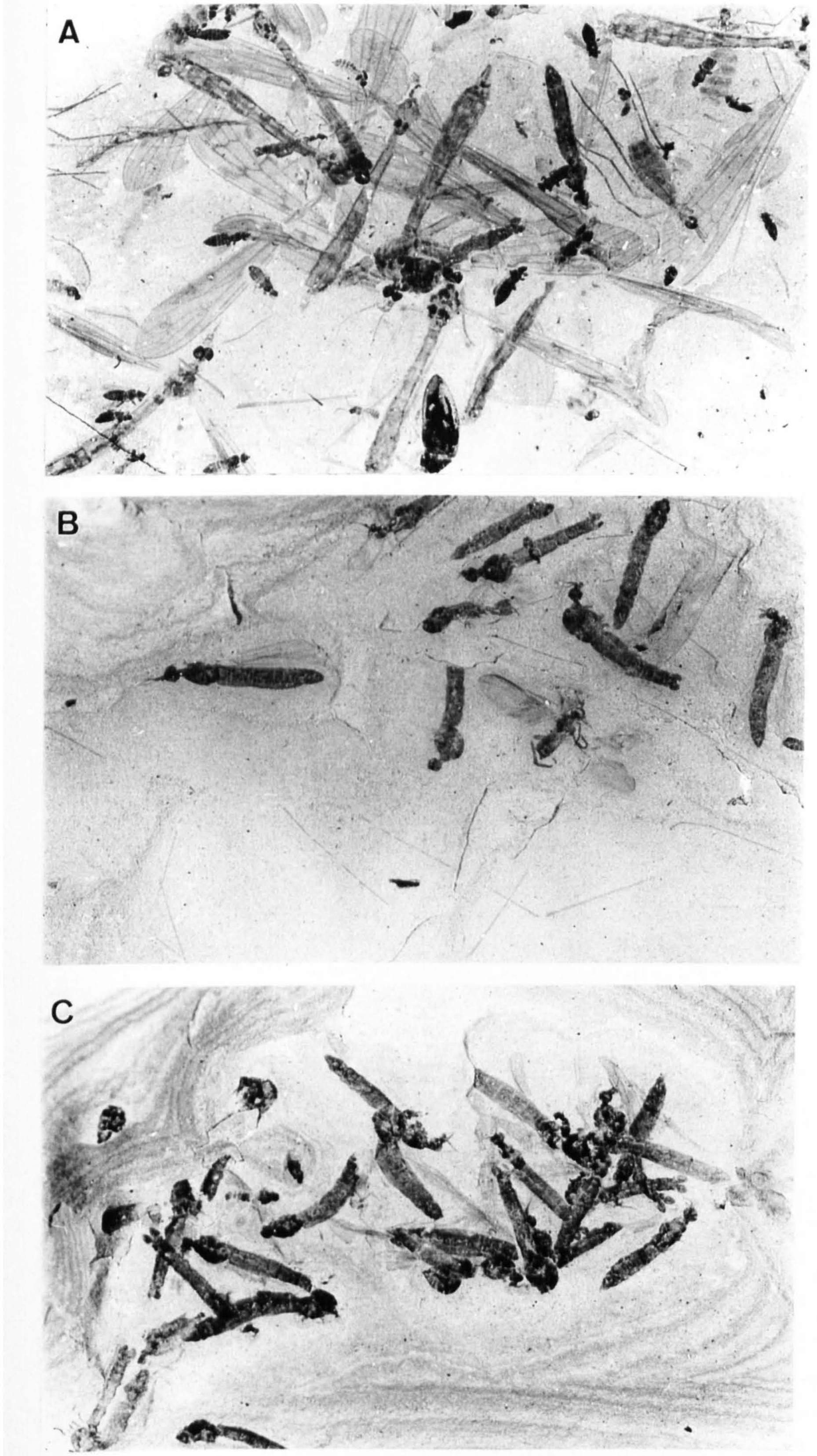


Figure 6.06 Relative proportions of insects recovered from the various sites of the Piceance Creek Basin since 1990.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ORDER	FAMILY	COMMON NAME	ECOLOGY
Odonata	Chlorocyphidae	damselfly	Found near/flying over still or slow flowing water. Habitats typically forested or meadow. Eggs laid under water. Nymphs aquatic. Typically only fragmentary wings recovered (Fig X).
	Calopterygidae	broad-winged damselfly	
	Libelludae	common skimmer dragonfly	
Blattodea	Blattidae	cockroaches	Generally tropical/subtropical. Found in damp leaf litter.
Orthoptera	Gryllidae	crickets	Prefer warm/hot conditions. Found in herbage/ leaf litter of woodland, meadow, scrub, grassland.
	Acrididae	short-horned grasshoppers	
Psocoptera		bark/booklice	Live either on leaves, twigs or under stones and in leaf litter.
Heteroptera	Reduviidae	assassin bugs	While many of these families live in the leaf litter or beneath stones others prefer the herbage layer. Saldidids are found in muddy environments around lakes and salt marshes. Gerrids prefer still/slow flowing water. The majority are herbivorous, feeding on phleom, although gerrids catch dead or drowning insects.
	Coreidae	leaf-footed bugs	
	Saldidae	shore bugs	
	Lygaeidae	seed bugs	
	Cydnidae	burrower bugs	
	Pentatomidae	stink/shield bugs	
	Gerridae	water striders	
	Gelastocoridae	toad bugs	

Table 6.1 Complete faunal list of the Green River insects, based upon the catalogues of Wilson (1978) and Lewis and Heikes (1991). The ecological interpretation is based on Imms (1973), McGavin (1992), Chinery (1993).

ORDER	FAMILY	COMMON NAME	ECOLOGY
Diptera	Tipulidae	crane fly	Dipterans occupy a range of environments. A number of families prefer moist wooded areas and meadows (Mycetophillidae, Stratiomyidae, Heleomyzidae, Chironomidae, Bibionidae) often close to standing water such as lakes or streams (Tipulidae, Culicidae, Empidae, Dolichopodidae, Heleomyzidae). Marshy areas are also a frequent habitat for both adults (Sciomyzidae) and larvae (Tabanidae). A number lay their eggs in standing water (Culicidae, Tabaridae, some Dolichopodidae, Syrphidae). Many families are attracted to flowers (Bibionidae, Syrphidae, Tephritidae, Anthomyidae, Muscidae, Stratiomyidae). Rank vegetation, leaf litter, rotting organic material and dung are also common habitats (Tachinidae, Heleomyzidae, Asilidae, Cecidomyiidae). Three families have a close association with mammals (Tabanidae, Sciomyzidae, Oestridae), with the oestrids often host specific.
	Culicidae	mosquito	
	Chironomidae	non-biting midge	
	Bibionidae	March fly	
	Cecidomyiidae	gall gnat	
	Sciaridae	dark-winged fungus gnat	
	Mycetophilidae	fungus gnat	
	?Tabanidae	horse fly	
	Stratiomyidae	soldier fly	
	Acroceridae	small-headed fly	
	Asilidae	robber fly	
	Empididae	dance fly	
	Dolichopodidae	long-legged fly	
	Platypezidae	flat-footed fly	
	Syrphidae	hover/flower fly	
	Cenopidae	thick-headed fly	
	Tephridae	fruit fly	
	Sciomyzidae	marsh fly	

ORDER	FAMILY	COMMON NAME	ECOLOGY
Diptera (cont'd)	Heleomyzidae	helomyzid fly	(see above)
	Anthomyidae	anthomyzid fly	
	Eophlebomyiidae	tsetse fly	
	Muscidae	muscid fly	
	Tachinidae	tachinid fly	
	Oestridae	bot & warble fly	
Trichoptera	Hydropsychidae	net-spinning caddisfly	Occur near rivers and lakes, often in significant numbers. Larval cases composed of conglomeration of small sand grains and gravel.
	Hydrophilidae	micro caddisfly	
	Limnephilidae	northern caddisfly	
	Sericostomatidae	sericostomatid caddisfly	
Lepidoptera	Yponomentidae	ermine moths	Closely associated with flowering plants both as larvae and adults.
	Thysididae	widow-winged moth	
Hymenoptera	Tenthredinidae	common sawflies	Hymenopterans occur in a range of habitats. Some prefer damp environments (Ichneumonidae) while others lead a parasitic life style (Braconidae). Many are found in association with flowering plants and fruit (Tenthredinidae, Ichneumonidae, Sphecidae). Ants are entirely social, and are often found in large swarms. Tend to occupy the leaf litter.
	Ichneumonidae	ichneumonid wasps	
	Braconidae	braconid wasps	
	Chalcididae	chalcidid wasps	
	Sphecidae	sphecid wasps	
	?Anthrophoridae	digger bees	
	Formicidae	ants	

ORDER	FAMILY	COMMON NAME	ECOLOGY
Homoptera	Cixiidae	cixid planthoppers	Found in grassy areas, meadows, pastures, woodland margins particularly near water. All are herbivorous, sucking liquid food from plants. Eggs tend to be laid inside the plants
	Delphacidae	delphacid planthoppers	
	Fulgoridae	planthoppers	
	Ricaniidae	ricanid planthoppers	
	Flatidae	flatid planthoppers	
	Cercopidae	froghoppers/spittle bugs	
	Cicadellidae	leafhoppers	
	?Aphididae	aphids	
	Pemphigidae	gall-making aphids	
Thysanoptera	Aeolothripidae	predaceous banded thrips	Commonly found in association with cruciferous/leguminous plants, grasses and conifers. Most are pollen feeders, although some are predaceous.
Mecoptera	Bittacidae	hangingflies	Found on low lying vegetation around woodland margins. Feed mainly on dead and dying insects.

representatives of the orders Isoptera, Dermaptera, Mantodea, Planipennia, Plecoptera and Collembola that await identification to family level (Pribyl *et al.* 1996). The table also includes an interpretation of the ecology.

The evidence of the entomofauna suggests a forested environment with damp leaf litter, open meadow and low scrub vegetation. Many of the families, as might be expected, are intimately associated with quiet water, whether as adults (*e.g.* Diptera: Tipulidae [Plate 6.4], Culicidae [Plate 6.5E], Empidae; Coleoptera: Dytiscidae, Hydrophilidae; Heteroptera: Gerridae; Odonata [Plate 6.5A]; and Ephemeroptera: Ragge 1965; Imms 1973; Evans 1975; Walsh and Dibb 1975; Stubbs and Falk 1983; Chinery 1993; Gullan & Cranston 1994), or juvenile stages (*e.g.* Coleoptera: Tabanidae; Diptera: Culicidae, Tabaridae; Trichoptera; Odonata; and Ephemeroptera: Imms 1973; Evans 1975; Wilson 1978; Miller 1979). Some families suggest a muddy/marshy shoreline (Heteroptera: Saldidae: Imms 1973; Wilson 1978).

The insects provide evidence of an associated biota that is not represented by fossils. The presence of mammals is suggested by the dipteran families Culicidae, Tabanidae, Eophlebomyiidae, Sciomyzidae and Oestridae (Miller 1983; Miller and Peck 1979). Insects that feed on carrion and dung also occur (Coleoptera: Staphylinidae [Plate 6.3F], Scarabaeidae, Nitulidae) (Miller and Peck 1979).

6.6 TAPHONOMY

6.6.1 Introduction

Although the taxonomy of the Green River insect fauna has received much attention over the last century, no attempt has been made to document the taphonomy. Often museum collections represent the best material and most complete specimens. Such collections do not allow an assessment of the conditions of decay and disarticulation. The collection of insects gathered from the Piceance Creek basin during the summer of '96 include all specimens regardless of completeness and therefore allow an assessment of the conditions of decay in the lake.

6.6.2 Degree of completeness

6.6.2.1 Method. Each of the fossils was examined and its length along the long axis measured. Completeness was categorized in a series of states (see Table 6.4). *Indet.* specimens are those which cannot confidently be assigned to any particular category, *e.g.* the elytra of beetles commonly conceal the state of completeness of the body, hind wings and legs.

State	Definition
Intact	Retains all major body components
Dissociated	Disarticulated components of still in association
Limbless	Specimens without legs but otherwise intact
Body	Only head, thorax and abdomen articulated
Wing	Disarticulated wing or elytra
Leg	Disarticulated leg
Abdomen	Disarticulated abdomen
Unknown	Specimens that cannot confidently be assigned to other categories

Table 6.4 Definition of terms of completeness.

6.6.2.2 Results. Greater than 80% of the specimens measure less than 12mm in length (Fig. 6.08). The majority of specimens (~30%) fall between 5-9mm. The largest specimens were Orthoptera (crickets) and certain Diptera (crane flies) at 26mm, but they were uncommon. The smallest specimens were less than a millimetre in size.

The insects display signs of only minimal decay (Fig. 6.07; *e.g.* Plate 6.3F, 6.4B-D). A half of all the specimens are intact and displayed no sign of abdominal rupture, a figure which rises to over 70% for certain orders (Orthoptera: 73%; Coleoptera: 81%; Fig. 6.07). The remaining specimens were predominantly appendage-less bodies of Diptera (particularly Tipulidae: 76%). Tipulid death assemblages, where the detached legs are still closely associated with the body, are common and suggest very quiet depositional conditions (a phenomenon in agreement with the sedimentological evidence: absence of cross bedding and current alignment of fossils, and only occasional minor rippling). Disarticulated wings, legs and abdomen constituted less than 10% of the total biota. The entomofauna of Paleoburn included a much higher proportion of insects which could not confidently be ascribed to other categories than the other sites (Fig. 6.06), due mainly to the nature of the preservation (see discussion of preservation below).

Blattodea and Orthoptera were commonly found intact (see Dayvault *et al.* 1995, Fig. 8, p. 104; Fig 6.07C, Plate 6.4B). Readily identifiable orthopteran legs and wings also occured, although no appendage-less bodies were recovered. Coleoptera were almost always intact (Fig. 6.07D; Plate 6.03). Disarticulated elytra accounted for less than 10% of the coleopteran total. Diptera, particularly Tipulidae (crane flies) and Bibionidae (March flies; Plate 6.4D) were commonly disarticulated (Fig. 6.07B). Tipulids, because of the ease with which their long, thin legs are shed are particularly sensitive to ambient environmental conditions (McGavin 1992). Tipulid death assemblages were relatively common (Plate 6.5), with complete specimens (A), examples lacking legs (B,C), and examples lacking all appendages.

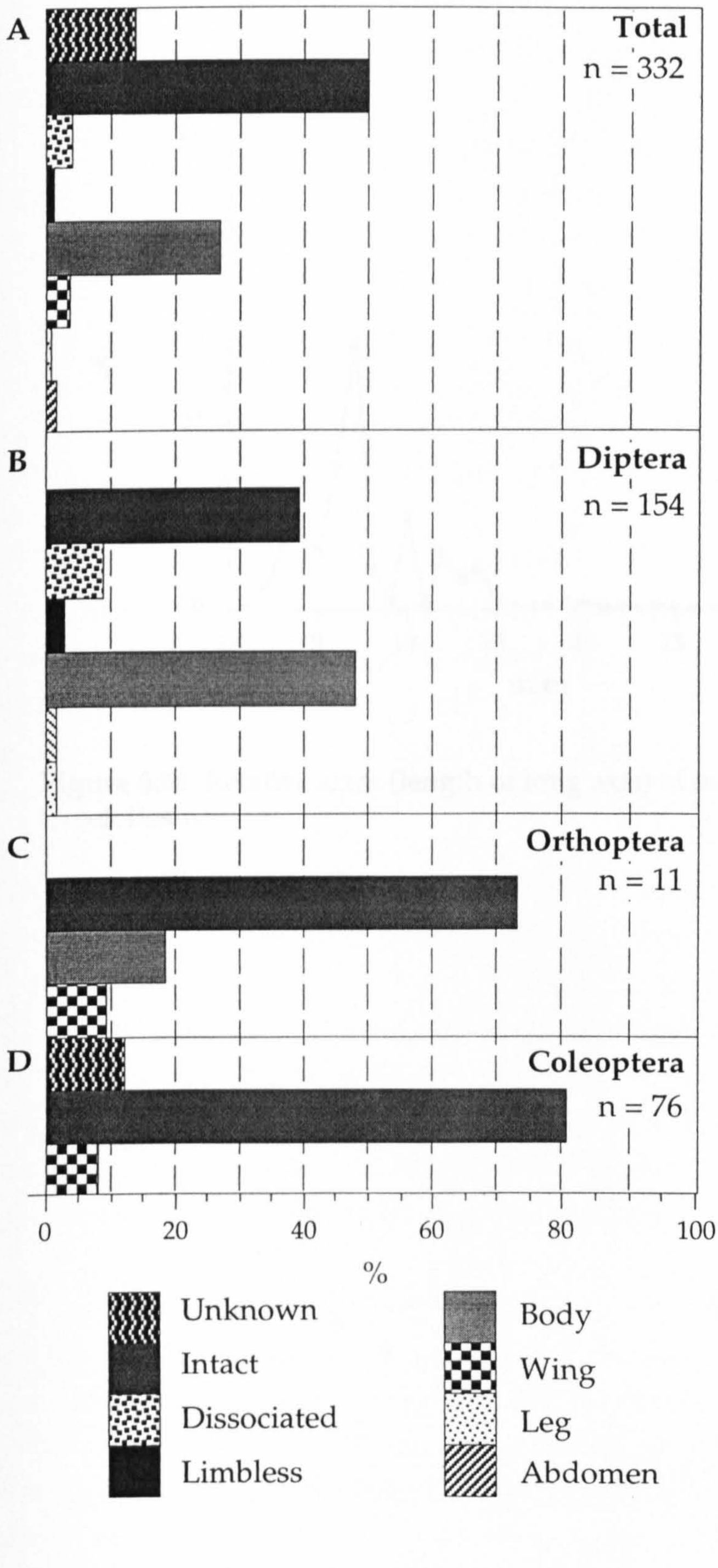


Figure 6.07 Relative intactness of the Piceance Creek specimens.

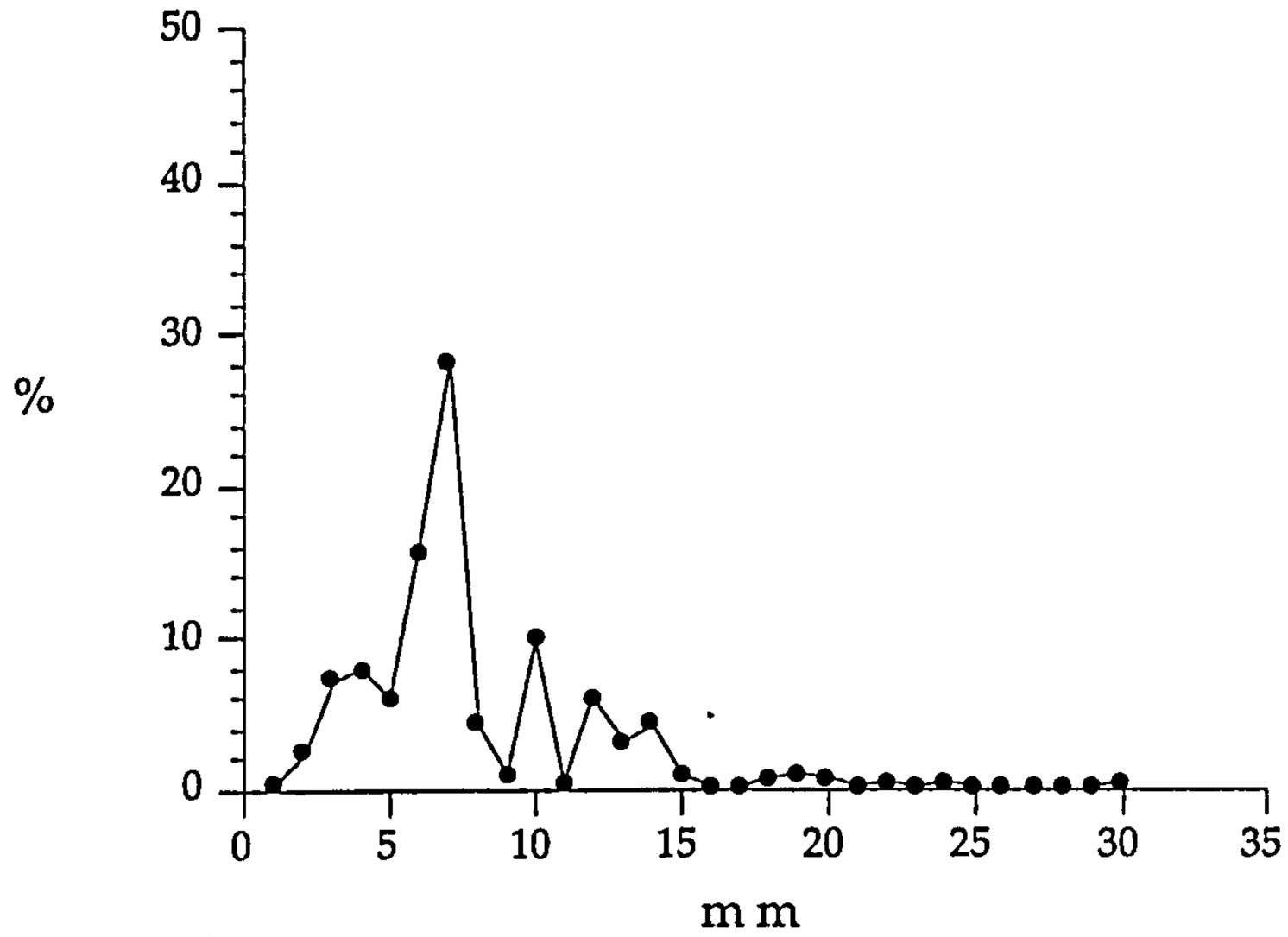


Figure 6.08 Relative sizes (length of long axis) of insects from the Piceance Creek Basin.

6.6.2.3 Depositional conditions.

The absence of significant numbers of large specimens, also noted by Cockerell (1921f), is unusual. Discovery of the occasional large individual indicates that such specimens were not entirely absent from the biota. This feature may reflect the relative ease with which large individuals of certain orders can move about the surface of still water and ultimately escape (see Martinez-Delclòs and Martinell 1990, 1993; Chapter 3). Living cockroaches are able to move about the water surface, and so avoid drowning (Chapter 3). Ants (Hymenoptera: Formicidae) and orthopterans are also known to 'move along the water surface without difficulty' (Martinez-Delclòs and Martinell, 1990; 1993, p. 135). However, members of the orders Coleoptera, winged Hymenoptera, Diptera and Lepidoptera, are unable to move about the surface (Martinez-Delclòs and Martinell 1990, 1993). The wings of the last three orders rapidly become trapped by the surface tension (see also Chapter 2).

Insects which decay on the surface would be expected to shed components over a wide area of the lake bottom. The shrimp decay experiments of Allison (1986) produced a 'carpet' of skeletal elements upon the vessel floor. A similar phenomenon would have occured in the experiments of Chapter 2 were it not for the cohesive nature of the enshrouding microbial film. However, the legs of Tipulidae are commonly found in close association with the body, a feat which would be highly unlikely if disarticulation occurred on the surface. Indeed it is unlikely that the detached tipulid legs would ever have the acquired the weight to break the surface tension of the water. Decay and disarticulation must therefore have occurred after submergence.

Submergence must have been relatively rapid, since prolonged residence on the surface would have left the carcass vulnerable to scavengers; birds (Grande 1994), reptiles and amphibia (Grande 1984; Dayvault *et al.* 1995), and fish (Grande 1984, 1989) have been all reported in the Piceance Creek basin. Since insect carcasses can remain buoyant for lengthy periods (see experiments of Chapter 2), the evidence for their rapid submergence in the Piceance Creek lake is problematic.

6.6.3 Fossil preservation

6.6.3.1 Introduction. The insects of the Piceance Creek basin are typically two dimensional organic fossils. Pribyl *et al.* (1996) claimed that some (but not all) of the specimens recovered from the Old Mountain site are pyritized. The remainder are organic. The fossils of the Paleoburn site are different. The majority of specimens, though still two-dimensional, are preserved by an iron mineral. The quality of preservation is poorer at Paleoburn than elsewhere in the basin. A number of small (<2cm), discoidal concretions, occasionally nucleated about insect and plant remains occur (Plate 6.2). The majority of such nodules are barren (>90%).

6.6.3.2 Material and methods. A representative sample of insects from the Anvil Points (n=20), Denson (n=10), Old Mountain (n=10) and Paleoburn (n=20) localities was selected for SEM and electron microprobe analysis. Matrix from around the specimens was subjected to XRD analysis. Attempts to extract sufficient organic material from the specimens, uncontaminated by the kerogen of the varves, were unsuccessful, precluding analytical pyrolysis.

Scanning electron microscopy (Appendix A1.1). Each specimen was coated with gold and examined under the SEM.

X-ray diffraction (Appendix A1.3). Samples of the matrix were excavated from two specimens from each site. Material was also excavated from within the 'nodules' of Paleoburn (n=3). The resultant relative peak intensities were used to calculate the approximate percentage by volume of each mineral in the oil shale.

Determination of weight % kerogen. Two small cubes of unweathered rock (1cm^3) from the Kohls site of Anvil Points and Paleoburn were cut using a fine diamond saw. To avoid the use of water as a lubricant, the samples were cut very slowly. Each sample was crushed, first in a vice, and thereafter with a mortar and pestle. A 100g sample was weighed out and placed in an oven at 110°C for 24 hours, to remove any water. The sample was re-weighed. The organic constituents were destroyed using hydrofluoric acid, following the method of Stanfield and Frost (1949). The sample was returned to the oven (110°C) for a further 24 hours and then re-weighed.

6.6.3.3 Results

Structural preservation. The specimens are composed of a thin (<10μm) film of amorphous organic material. This film drapes the underlying grains of sediment, giving a surface texture superficially similar to that of the surrounding matrix. Consequently, the fossil is often difficult to distinguish from the matrix under the SEM (Plate 6.6A). Examination using backscattered electrons reveal the extent of the organic material (Plate 6.6B). Structure is preserved only in the cuticle of beetle elytra and pronota. Architecture such as striations, pits and protuberances occur although they are often indistinct. The specimens from Old Mountain are also composed of structureless organic material Microprobe analysis failed to reveal the presence of pyrite, and no pyritic fabric was observed. The typical Paleoburn specimens consist of a thin (<0.1mm) mineral layer which replicates the outline of the specimen but preserves no recognisable cuticle structure, save the architecture of beetle elytra and pronota (Plate 6.6C). Backscatter electrons reveal the extent of mineral replication (Plate 6.6D).

The concretions of Paleoburn range from 7-16mm. They are dissected by fine micro-septaria (Plate 6.2A). The boundary between nodule and matrix can be extremely irregular (Plate 6.2B). There is often a red halo around each concretion which extends for no more than 3mm. The majority of Paleoburn concretions are not fossiliferous. In those which are, beetles (Plate 6.2D-F) and wood fragments are the only recognizable

quartz and a depletion of ankerite at the latter site. A significant amount of haematite also occurs in the Paleoburn sample.

6.7 DISCUSSION

6.7.1 Introduction

The insects of the Piceance Creek basin (with the exception of those from Paleoburn) are preserved in a manner similar to those of the other Green River localities. Therefore, the following discussion is almost certainly broadly applicable to all of the Green River lakes. However, since the various lakes varied in size, depth, character and longevity, care must be taken when applying the findings beyond the Piceance Creek basin.

The insects of the Piceance Creek basin must have undergone a rapid submergence and entombment to protect the specimens from scavenging and mechanical destruction. Decay must also have been inhibited rapidly. Only the sclerotized coleopteran cuticle retains any structure. Although sclerotized cuticle may retain its structure (and biochemical signature) for thousands of years (Miller *et al.* 1983; Stankiewicz *et al.* 1997c; Chapter 8), non-sclerotized cuticle has a considerably shorter life span (see Chapter 2, section 2.7). Okafer (1966b) estimated that non-sclerotized cuticle was unlikely to survive more than a year of burial. The process of fossilization must, therefore, have commenced within a comparable period. The fossilization of the Green River insects must therefore be closely linked with the formation of kerogen.

The insects of Paleoburn are distinctly different from those of the Green River Formation. Their characteristic form must be attibuted to a later, localised, phase of alteration.

6.7.2 Kerogen formation

The economic importance of kerogen-derived oil has ensured that a number of organic geochemical studies have been conducted in an attempt to understand its formation (see Yen and Chilingham 1976, and references therein; Tissot and Welte 1984). Early work suggested that kerogen formed as the result of a series of consecutive and random re-polymerization and polycondensation reactions of a very small fraction of the degradation products of the biomass (Durand 1980; Tissot and Welte 1984). Such newly formed (proto)kerogens continuously underwent chemical transformations becoming increasingly condensed and insoluble in the process.

An alternative approach focused on the chemical and structural identification of organisms such as algae (Largeau *et al.* 1990; Derenne *et al.* 1991a, b; Douglas *et al.* 1991), terrestrial plants (*e.g.* Nip *et al.* 1986a, b; Tegelaar *et al.* 1991), or soil microbes (Lichfouse *et al.* 1996). This led to the development of a different model of kerogen formation involving the selective preservation of insoluble and non-hydrolyzable biomacromolecules protected within the envelopes of a number of organisms that are

nuclei. Structural detail is preserved only in the elytra and pronota of the beetles (Plate 6.7A-D). Although much of the basic form of the beetle is destroyed, patches of higher fidelity preservation occur. Layers of the procuticle are preserved, although no microfibril structure is retained (Plate 6.7A,B). Wrinkles in what appears to be the arthrodial membrane are also evident (Plate 6.7C, D). The texture of the non-fossiliferous nodules is similar to that of the matrix.

General mineralogy of sedimentary matrix. The sediment of the Piceance Creek basin is a mixture of quartz and carbonate minerals (Fig. 6.09; Table 6.4). The predominant clastic mineral of the oil shale is quartz (Fig 6.09), which commonly occurs as sharply angular or subangular grains (Bradley 1931). Carbonate minerals are also common, and are dominated by ankerite. Calcite, plagioclase and K-feldspar also occur.

Mineral	**Bradley[a]**		**Ingram *et al.*[b]**	**This study[c]**	
Quartz	12	10	13	14	40
Ankerite	32	9	18	22	31
Calcite	7	<1	2	7	5
K-feldspar	7	2	6	6	8
Plagioclase	-	-	6	4	4
Clay	-	21	1	-	-
Analcite	17	-	1	-	-
Pyrite	2	2	1	-	-
Haematite	-	-	-	<1	11
Organic matter (minus combined water	22	46	51	44	-
Total	**99**	**90**	**99**	**96**	**99**

[a]Bradley 1931 - The first sample was obtained from 'just below' the Mahogany Zone, Monarch Shale Oil Co. mine, Piceance Creek basin, the second from the Mahogany Zone, near the head of the East Middle Fork of Parachute Creek, Piceance Creek basin.

[b]Ingram *et al.* 1983 - The sample was obtained from the Mahogany Zone of the Colony Mine, Piceance Creek basin.

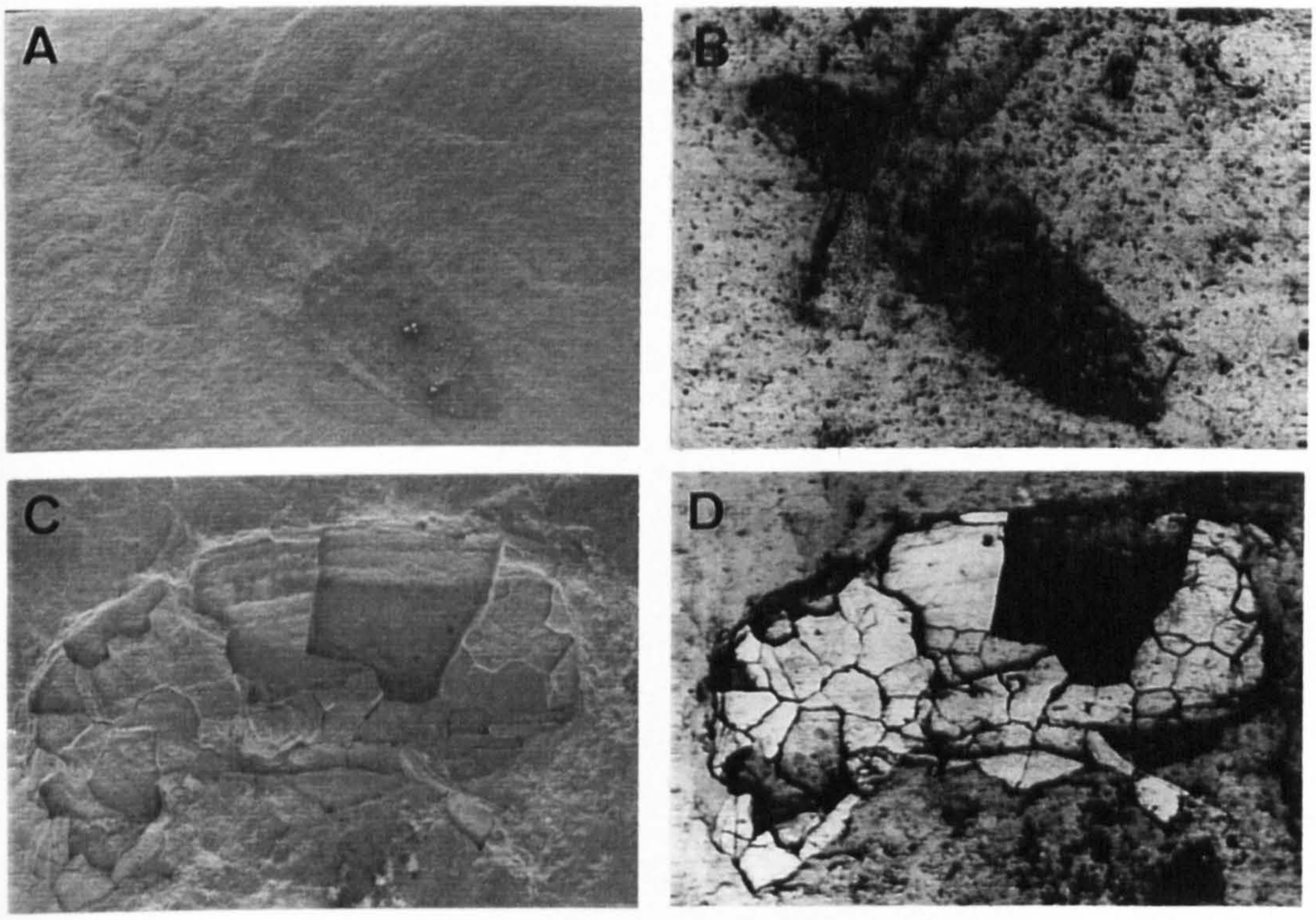
[c]The first sample was obtained from the Kohls site, Anvil Points (see above). The second sample was obtained from the Mahogany Zone, Paleoburn.

Table 6.5 Percentage mineral composition of the oil shale.

Significant differences exist between the oil shale of the Anvil Points and Paleoburn localities. The Anvil Points oil shale contains up to 44% weight percent kerogen, whereas the sediments of Paleoburn are retorted of all organic material. While the relative proportion of minerals in the Anvil Point sample analysed is in broad agreement with the findings of other studies (Bradley 1931; Ingram *et al.* 1983), there are significant differences between the Anvil Points and Paleoburn localities, notably in terms of the relative proportion of ankerite and quartz. If the weight percent of the Anvil Point sample is corrected for the presence of kerogen, the relative proportion of quartz/ankerite is 27/42, compared to a ratio of 40/31 for Paleoburn, indicating a relative enrichment of

Plate 6.6 Photomicrographs of Piceance Creek insects. A & B, SEM images of a Staphylinid (Coleoptera) from the Labandeira site. A, Using secondary electron beam, the fossil is difficult to discern. x14. B, Using backscatter electrons, the extent of organic replication can clearly be seen. x14. C & D, SEM images of a Curculionid (Coleoptera) from Paleoburn. C, Using secondary electron beam, the fossil is difficult to discerned. x14. D, Backscatter electrons reveal the extent of mineralization. x14. All specimens in the personal collection of author.

Plate 6.7 Microstructure of Paleoburn beetles. A, Ornamentation of epicuticle (left), and fabric of underlying matrix (right). x450. B, Layers within cuticle. x350. C & D, Wrinkles in the ?arthrodial membrane. x225, x900. All specimens currently in the personal collection of author.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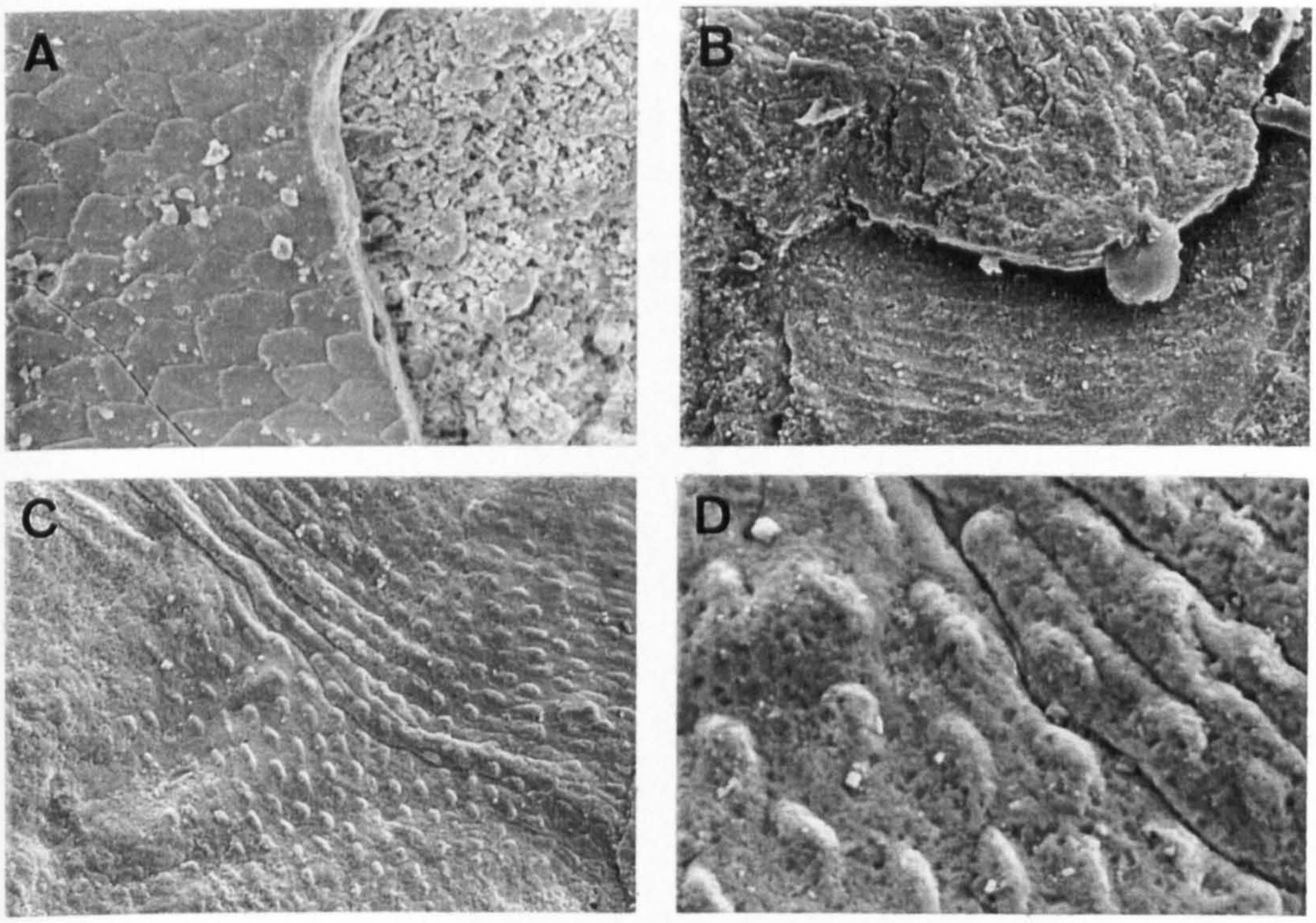
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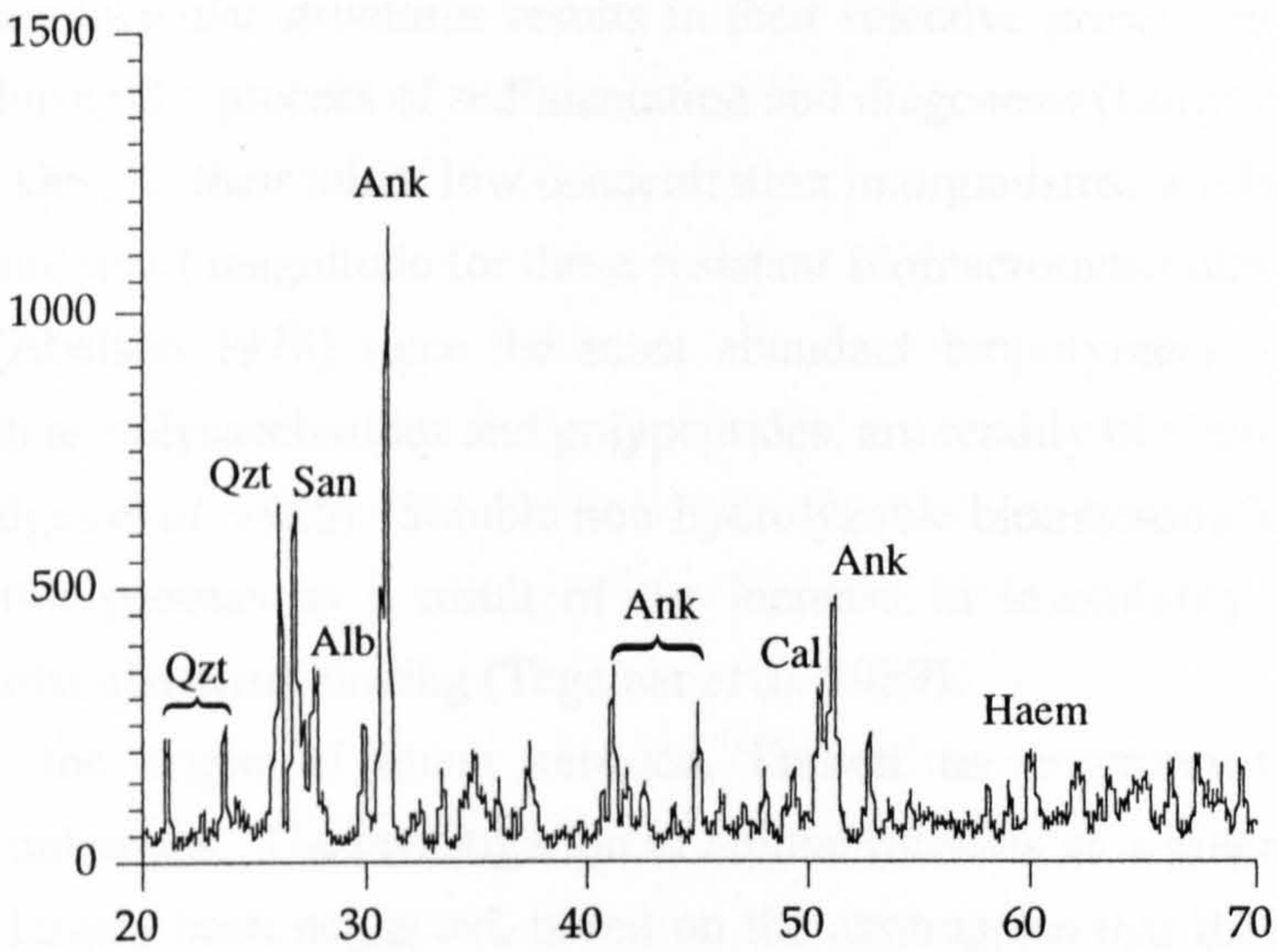
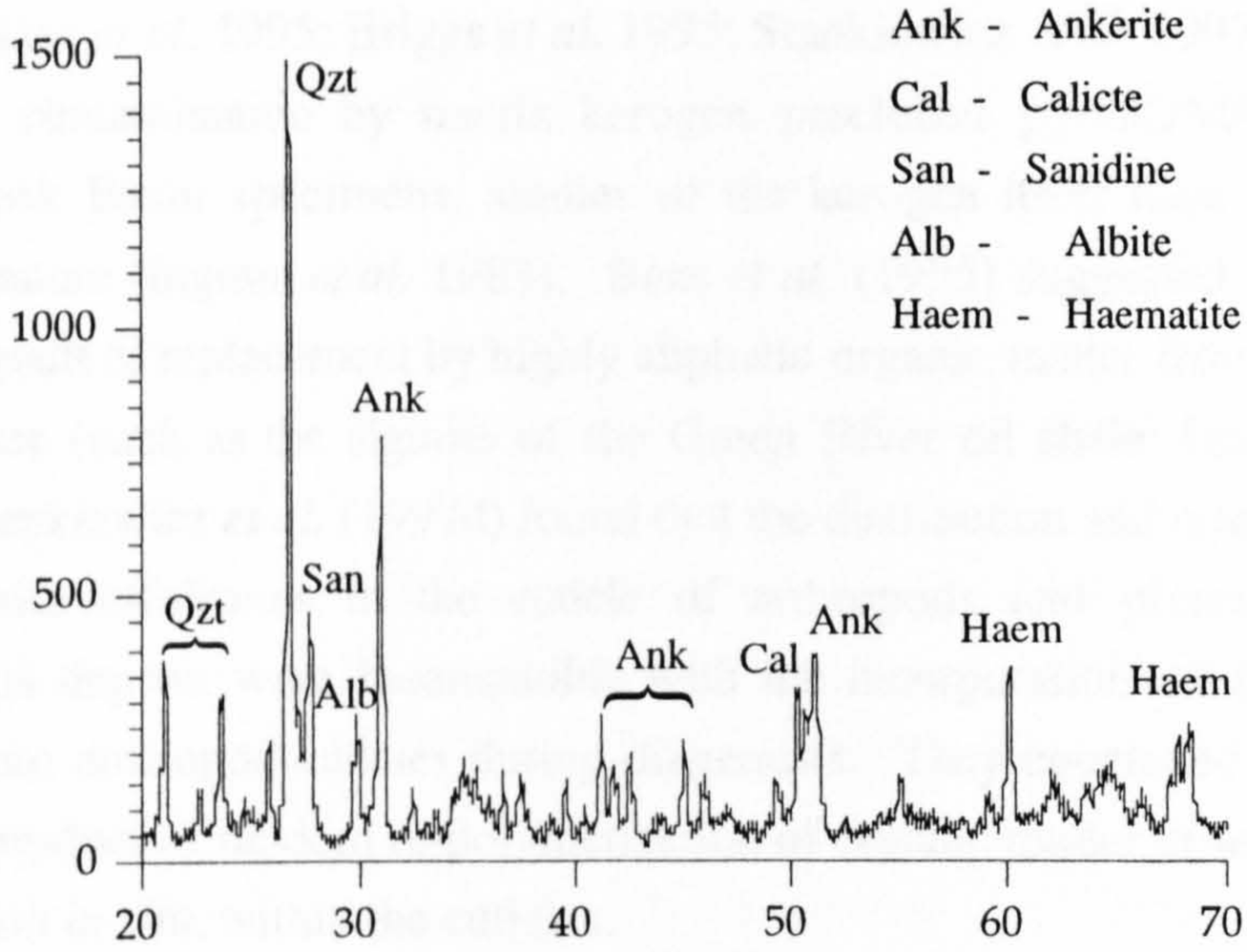
Anvil Points



Paleoburn



Qtz - Quartz
Ank - Ankerite
Cal - Calicte
San - Sanidine
Alb - Albite
Haem - Haematite

Figure 6.09 X-ray diffration patterns of whole rock from the Piceance Creek basin. The Anvil Points trace is typical of the other sites.

highly resistant to degradation (see Nip *et al.* 1986a, b; Goth *et al.* 1988; Tegelaar *et al.* 1989; de Leeuw *et al.* 1991; Stankiewicz *et al.* 1997a, b). The high survival potential of such biomacromolecular structures results in their selective preservation and consequent enrichment during the process of sedimentation and diagenesis (Largeau *et al.* 1986; Goth *et al.* 1988). Despite their initial low concentration in organisms, a relative enrichment of two to three orders of magnitude for these resistant biomacromolecules during diagenesis is possible (Abelson 1978) since the most abundant biopolymers occurring in extant biomass, such as polysaccharides and polypeptides, are readily biodegraded (see Given *et al.* 1984; Hedges *et al.* 1985). Soluble non-hydrolyzable biomacromolecules may also be involved in this process as a result of the increase in insolubility brought about by advancing molecular cross-linking (Tegelaar *et al.* 1989).

However, the origin of much kerogen, known as amorphous organic material (A.O.M.), is unknown. The investigation of animal remains as a potential source of this A.O.M. has largely been neglected, based on the assumption that they are characterized by poor preservation potential, and make only a limited contribution to sedimentary organic matter (Stankiewicz *et al.* 1997d, in review). Only recently has it been shown that macromolecules derived from invertebrate tissues may be preserved in ancient sediments (Baas *et al.* 1995; Briggs *et al.* 1995; Stankiewicz *et al.* 1997b, c, d in review).

Although contamination by matrix kerogen precluded py-GC/MS analysis of the Piceance Creek Basin specimens, studies of the kerogen itself have revealed a highly aliphatic signature (Ingram *et al.* 1983). Baas *et al.* (1995) suggested that altered cuticle may be the result of replacement by highly aliphatic organic matter from an external plant or algal source (such as the alginite of the Green River oil shale: Hutton *et al.* 1980). However, Stankiewicz *et al.* (1997d) found that the distribution and relative abundance of long-chain alkenes/alkanes in the cuticle of arthropods and plants from the same Carboniferous deposit were incompatible with the incorporation of molecular material from plant into arthropod cuticles during diagenesis. They concluded that the alteration was not the product of random re-polymerization of organic matter in sediment, but rather polymerization *in situ*, within the cuticles.

The only aliphatic substances found in insects are the lipids or waxes of the cuticle which comprise about 5% of cuticular mass (Kolattukudy 1976). Polymerization within the cuticle (see Stankiewicz *et al.* 1997d, in review) is consistent with both the aliphatic composition of the Green River kerogen and with the absence of distinctive ultrastructure in the fossils. This absence may be due to degradation of non-waxy constituents which form the bulk of the cuticle, leaving behind polymerized aliphatic cuticle. However, the destruction of an organism's original chemistry need not imply destruction of its morphology (see Chapter 7, section 7.3). Specimens that retain exceptional morphology but altered chemistry are common (Bartram *et al.* 1987; Voight 1988; Schaal and Ziegler 1988; Stankiewicz *et al.* 1997a, d in review; McCobb *et al.* 1997, in review). It is possible that decay alone could be responsible for the morphological destruction of non-

sclerotized cuticle, and the inhibition of decay thereafter for the survival of the sclerotized tissues (see Chapter 2). Whatever the process of transformation it is clear that sclerotization of the cuticle imparts a greater chance of survival. The processes of organic conversion to more recalcitrant biomolecules is presently the subject of an intensive study at Bristol University (see Stankiewicz *et al.* 1996, 1997a, b, c, d in review, e in review).

6.7.3 Post-lithification alteration

Although the sediments of Paleoburn are similar to those of the other sites, there are a number of significant differences. The red-stained sediments are devoid of kerogen. Nahcolite has been leached from a narrow zone of vugs (although it is commercially exploited from correlative horizons where leaching has not occurred elsewhere in the Piceance Creek Basin: Cole 1983). The passage of water is suggested by darker stains perpendicular to bedding. The mineralogy of the Paleoburn matrix, though broadly comparable to that of the other sites, has a higher iron (haematite) content. The fossils are also devoid of organic matter. Replicated by a fine layer of haematite, the quality of preservation is poor compared with the other sites. Only the beetles display any microstructure. Haematite is a common oxidation product of metasomatism and is readily mobilised by the passage of ground water (Deer *et al.* 1983). Iron-saturated pore waters may be responsible for the alteration at the Paleoburn locality, with haematite precipitating out of solution onto the organics of the proto-kerogen.

The presence of a band of occasionally fossiliferous iron nodules is also a marked difference. They are generally barren and are restricted to a slightly coarser, more laterally porous horizon, which presumably accounts for their discoidal shape (see Allison 1991 for discussion). Their growth appears to destroy progressively the organic remains about which they nucleate leaving only patches of cuticular structure behind, unlike the syn-sedimentary nodules of the Mazon Creek (see Chapter 4). The size of the fossil-bearing nodule is closely related to the size of the organic nucleus.

Coleoptera (and wood) are the only recognizable nuclei. However, this is probably a taphonomic effect since it is unlikely that the fauna consisted solely of beetles. Other taxa occur in close proxomity. It is probable that only sclerotized insects (and wood) are able to survive the destructive formation of the concretions. Although much detail is lost, occasionally what remains is of a higher fidelity than the preservation noted at the other sites. The preservation of layers within the procuticle, and wrinkles in the ?arthrodial membrane indicate that the concretions offered protection from the processes that destroy these features elsewhere.

The Old Mountain specimens, from which the organic film has been partially removed, are almost certainly the result of biogenic alteration resulting from the action of the vegetation immediately atop the outcrop. Web-like rootlets frequently cover the upper bedding planes, to which the altered specimens are restricted. No pyritization is evident (*contra* Pribyl *et al.* 1983).

CHAPTER 7

3-D PRESERVATION: RIVERSLEIGH and BEMBRIDGE

The findings of this chapter are reported in

Duncan, I.J. and Briggs, D.E.G. (1996) Three-dimensionally preserved insects from the Tertiary of Riversleigh, Australia. *Nature*, 381, 30-31.

Duncan, I.J., Briggs, D.E.G and Archer, M. (1997) Insects and millipedes from the Tertiary of Riversleigh, Queensland, Australia. *Palaeontology* (submitted).

McCobb, L.E., Duncan, I.J., Jarzembowski, E.A., Stankiewicz, B.A., Wills, M.A. and Briggs, D.E.G. (1997) Taphonomy of the insects of the Bembridge Marls (Late Eocene), Isle of Wight, England. *Geol. Mag.*

7.1 INTRODUCTION

7.1.1 Three dimensional preservation

While fossil insects are rarely totally compressed, uncompacted specimens are uncommon. Three-dimensional preservation normally relies on sufficiently early mineralization to prevent collapse through decay, and to protect the fossil from overburden-induced compaction. Thus insects preserved as organic remains are rarely three-dimensional, except in conservation traps (sensu Seilacher *et al.* 1985) such as amber (Poinar and Hess 1982; Henwood 1992, 1993; Grimaldi *et al.* 1994), peat (Elias 1993) and asphalt (Miller 1983; Stock 1992; Stankiewicz *et al.* 1997c). The insects of the Eocene Bembridge Marls, Isle of Wight, England (Jarzembowski 1980; McCobb *et al.* in prep.) are an exception. Here they are preserved essentially as a void left by the decayed internal tissues, lined with the cuticle, which is represented by a micron thick, highly altered, organic layer. Rarely are pre-Quaternary insects reported which preserve any vestage of original, unaltered organic material (although see Stankiewicz *et al.* 1997b). The chitin/protein of the cuticle is generally replaced by aliphatic and aromatic biomolecules (see Stankiewicz *et al.* 1997a). Doubt has even been cast upon presence of chitin in amber insects (Austin 1997; D.E.G. Briggs, *pers. comm.*).

Most three-dimensionally preserved insects occur in early diagenetic concretions, such as the siderite nodules that are known from a variety of Carboniferous sites (see Bolton 1905; Woodward 1907; Heyler 1980; Baird et al. 1985a, b), notably at Mazon Creek in

northeastern Illinois (Richardson 1956; Johnson and Richardson 1966; Nitecki 1979; Baird *et al* 1985a; Chapter 4). These Carboniferous insects rarely preserve ultrastructural details of the cuticle (see Baird *et al.* 1985a) in contrast to insects preserved in Tertiary concretions. Calcareous nodules from the Miocene of Barstow, California (Palmer 1957) exhibit micron scale-replication of the cuticle and internal tissue by a suite of minerals including quartz, apatite, celestite, gypsum and zeolite (Park 1995). The concretions of the Eocene London Clay, England, which are composed of pyrite, apatite or calcite (Britton 1960; Allison 1988), have yielded various beetles (Britton 1960), and a pyritized maggot (Rundle and Cooper 1971) which preserves surface details of the cuticle, but not the internal tissues. Phosphatic concretions from the mid-Tertiary Dunsinane Site at Riversleigh preserve insects (D. A. Arena *pers. comm.*).

The Riversleigh insects are exceptional in that phosphatization of the cuticle has led to three-dimensional preservation without the formation of a concretion. Phosphatized insects have also been reported from the Eocene Quercy Phosphorites of France (Handschin 1944), and the Oligocene fissure fillings of Ronheim, Germany (Hellmund and Hellmund 1996), but in both cases crystallization is coarser than at Riversleigh and less detail is preserved. A similar style of preservation in calcite is known from the Miocene volcanic deposits of Rusinga and M'fwangano Islands, Lake Victoria, Kenya (Leakey 1952, 1963) but only the gross morphology of taxa with thickened cuticles, such as millipedes and beetles, is preserved. Calcified millipedes are also known from Holocene cave deposits in the West Indies (Donovan and Veltkamp 1994), but the cuticle is likely to have been biomineralized in life.

7.1.2 Aims

Although three-dimensional fossil insects often preserve remarkable morphological fidelity, and have been the subject of much taxonomic interest (see above), little taphonomic research has been conducted upon them. To date, the principle studies have examined insects preserved in concretions (see Chapter 4; Park 1990, 1995) and amber (Henwood 1992, 1993). This chapter investigates insects recovered from two lagerstätten, the Upper Site of Riversleigh, Australia and the Bembridge Marls Insect Bed of the Isle of Wight, England, in an attempt to document the early diagenetic processess responsible for their preservation. The phosphatized insects of Riversleigh are examined, the resultant mineral fabrics documented and the mechanism of formation discussed. Some of the insects of the Isle of Wight, retain organically preserved cuticle, and mineralized internal tissue. The biogeochemistry of the cuticle is documented and the mechanism of formation discussed.

7.2 RIVERSLEIGH

7.2.1 Introduction.

To date, the importance of the Tertiary deposits of Riversleigh (north-west Queensland, Australia; Fig. 7.01) has stemmed from the remarkable mammals recovered, nearly trebling the number of mammal species recorded from the entire Australian continent (Archer and Bartholomai 1978; Archer and Clayton 1984; Archer *et al.* 1994a, b, 1995). The discovery of insects owes much to serendipity. Following acetic acid digestion of the vertebrate-packed limestone, the first arthropods were recovered by workers searching the insoluble residue for small bones and teeth. This discovery has increased the importance of the site, while improving a sparse Australian Tertiary insect record.

7.2.2.1 Australian insect record. The earliest Australian insects occur in an Upper Permian coal horizon at Belmont and in the Warner's Bay area north of Sydney (Knight 1950; Riek 1968; Fig. 7.01), where beds of hard, fine-grained chert contain many specimens, notably Mecoptera-Neuroptera and Homoptera-Psocoptera. Other orders are represented by only one or two specimens, sometimes too fragmentary for specific description (Riek 1970b).

Triassic insects have been recovered from a number of Australian localities. The best documented are from the Upper Triassic Mount Crosby-Denmark Hill horizons in south-eastern Queensland (Evans 1956, 1961, 1963; Riek 1955, 1956; Fig. 7.01), and the mid-Triassic Brookvale deposits of New South Wales (Riek 1954b). The Mount Crosby fauna is dominated by Blattodea and Homoptera, and certain panorpoid orders are also present (Riek 1955). The Denmark Hill horizons are not widely separated stratigraphically from those of Mount Crosby; about half the specimens recovered are Coleoptera, with Blattodea and Homoptera the other important components (Riek 1956). The remains at Brookvale are mostly beautifully preserved orthopteran wings; Mecoptera, Homoptera and Blattodea are also represented (Riek 1954b). Approximately 100m above this Brookvale horizon lie the Wiannamatta Shales from which fragmentary and poorly preserved insect remains, mainly beetle elytra, have been recovered (Riek 1970a). Fragmentary insect remains (a tegmen of a cockroach and a homopteran wing) have been recovered from Triassic coal measures in Hobart, Tasmania (Riek 1962, 1967a) and beetle elytra and part of a mesoblattinid cockroach have been reported from River Hill, Western Australia (Riek 1970a, b).

Uncertainty exists regarding the only possible Jurassic insect *Cicada lowei* from the Talbragar River fish-bed, near Mudgee, N.S.W., and an early Cretaceous age is possible (Riek 1970b; Fig. 7.01). The specimen is not a cicada and should most probably be referred to the Cercopoidea (Hemiptera) (Riek 1970b).

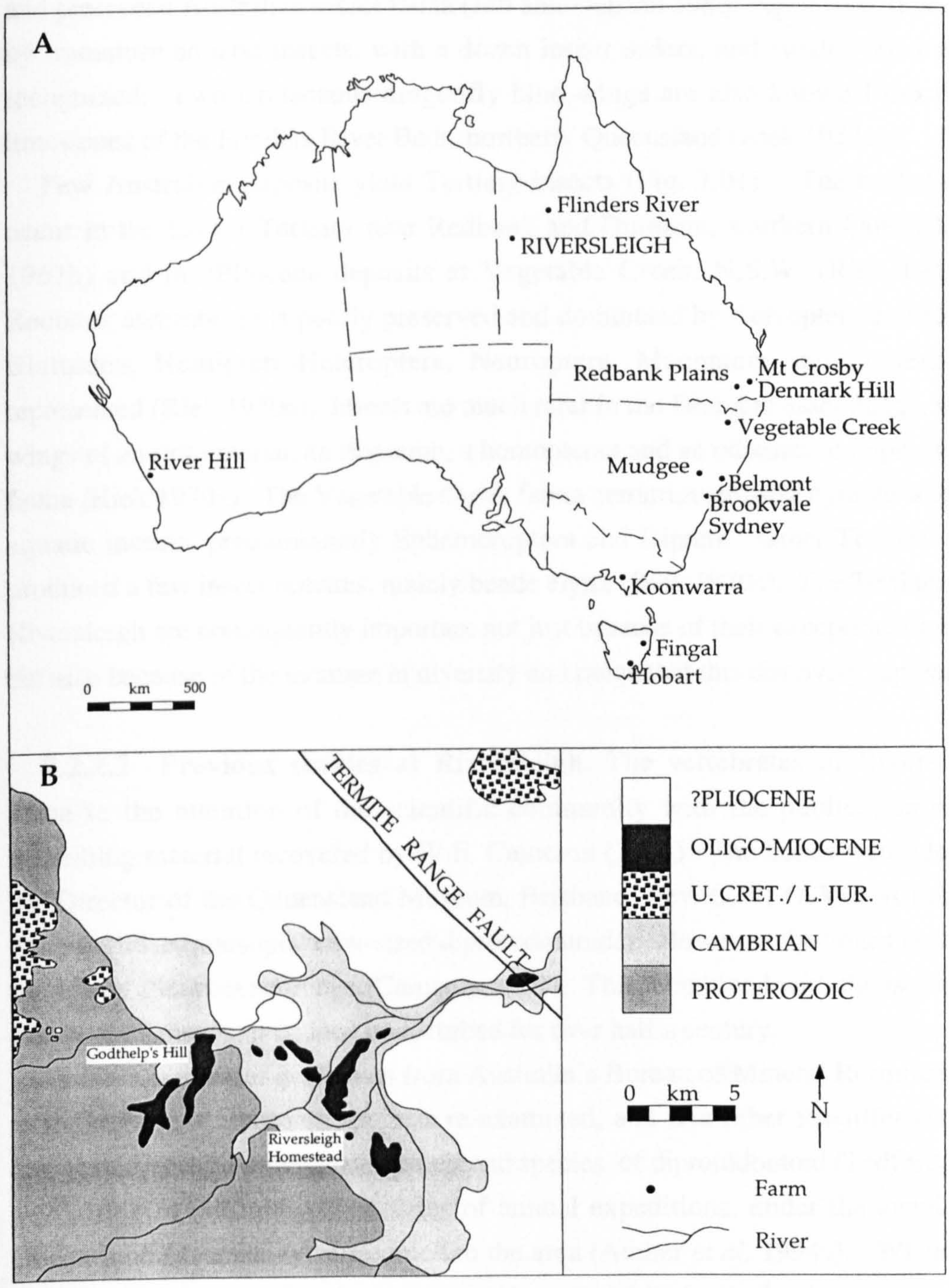


Figure 7.01 A, Principal insect lagerstätten of Australia. Riversleigh is printed in capitols. (After Reik 1970a). B, Detailed map of Riversleigh area detailing location of Godthelp's Hill (Upper Site), and surrounding geology. (After Megerian 1992).

The Lower Cretaceous Koonwarra Fossil Bed of Victoria yields the best documented and preserved Australian insect fauna (Jell and Duncan 1986; Fig. 7.01). It is dominated by immature aquatic insects, with a dozen insect orders, and sundry other arthropods recognized. Two Cretaceous dragonfly hind wings are also known from the marine limestones of the Flinders River Beds, northern Queensland (Riek 1954c).

Few Australian deposits yield Tertiary insects (Fig. 7.01). The best documented occur in the Lower Tertiary near Redbank and Dinmore, southern Queensland (Riek 1967b) and in ?Pliocene deposits at Vegetable Creek, N.S.W. (Riek 1954a). The Redbank assemblage is poorly preserved and dominated by Coleoptera and Homoptera; Blattodea, Hemiptera-Heteroptera, Neuroptera, Mecoptera and Diptera are also represented (Riek 1970*a*). Insects are much rarer in the Dinmore assemblage, with single wings of an orthopteran, an isopteran, a homopteran and an odonatan comprising the total fauna (Riek 1970a). The Vegetable Creek fauna comprises mostly nymphs and larvae of aquatic insects, predominantly Ephemeroptera and Diptera. Other Tertiary sites have produced a few insect remains, mainly beetle elytra (Riek 1970a). The Tertiary insects of Riversleigh are consequently important not just because of their exceptional preservation but also because of the increase in diversity and range that this discovery represents.

7.2.2.2 Previous studies at Riversleigh. The vertebrates of Riversleigh first came to the attention of the scientific community with the publication of a paper describing material recovered by W.E. Cameron (1901). The bones were identified by the Director of the Queensland Museum, Brisbane, Rev. C.W. DeVis, as belonging to Nototheriidae (marsupial cow-sized diprotodontoids). However, the bones were believed to be only Pleistocene in age (Cameron 1901). This, combined with the isolation of the site ensured the site remained undisturbed for over half a century.

In 1963, a team of geologists from Australia's Bureau of Mineral Resources returned to the region. Cameron's site was re-examined, and five other fossiliferous localities discovered, one of which yielded a second species of diprotodontoid (Tedford 1967).

Starting in the mid 70's a series of annual expeditions, under the auspices of the Queensland Museum, have returned to the area (Archer *et al.* 1994a). Whereas earlier expeditions recovered only bones easily extricable from the limestone, the Q.M. geologists removed the limestone as well using light explosives! The limestone blocks were then transported back to Brisbane where they were acid digested. The resultant bone material has significantly increased our knowledge of Australian mammals (Archer *et al.* 1994). Material recovered from the Gag Site alone , discovered in 1983, has nearly doubled the sum of previous knowledge of the diversity of Australia's Tertiary mammals (Archer *et al.* 1994)

Under the direction of Michael Archer of the University of New South Wales, Riversleigh is now recognized as the pre-eminent Australian vertebrate lagerstätte. To date almost a 100 papers have been published on the new and extraordinary marsupials of

the site (see Archer and Bartholomai 1978; Archer and Clayton 1984; Archer *et al.* 1994a, b, 1995 and references therein). In 1990, Riversleigh was declared a World Heritage Site (Archer *et al.* 1994a).

The insects have, so far, received less attention. Discovered by accident in 1987 the specimens were preliminarily identified by Peter A. Jell of the Queensland Museum (Archer *et al.* 1989, 1994). They have subsequently been documented and re-described by Duncan and Briggs of the University of Bristol, England (Duncan and Briggs 1996; Duncan *et al.* 1997).

7.2.2 Geological Setting

7.2.2.1 Introduction. Although Riversleigh was originally thought to represent a single, mid-Miocene assemblage (Tedford 1967), fossils from over two hundred distinct sites are now recognized, representing at least three distinct periods of Oligo-Miocene age, defined by Archer *et al.* (1989) as Systems A-C (A: late Oligocene - early Miocene; B: early - middle Miocene; and C: middle - late Miocene). The arthropod specimens discussed here were recovered from the System A limestones of the Upper Site of Godthelp's Hill (Late Oligocene/Early Miocene) (Fig 7.02). A single Pliocene assemblage, Rackham's Roost and numerous Pleistocene cave and riverine assemblages are also noted (Archer *et al.* 1989).

Although the underlying Cambrian and Precambrian units of the region are easily traced (Tedford 1967; Archer *et al.* 1989; Megerian 1992), correlation of the overlying Tertiary sediments has proved problematic. The isolated nature of the deposits, combined with an apparant lack of time-specific macroscopic sedimentary features has hampered attempts to trace boundaries (Archer *et al.* 1989). The problem is compounded by local cycles of deposition such that events "may have repeated themselves at different times in isolated areas" (Archer *et al.* 1989, p48). For these reasons the Tertiary biostratigraphic units of Riversleigh have been defined primarily on the basis of their faunas rather than their petrology. For a detailed discussion of the stratigraphy, see Megerian (1992).

7.2.2.2 Upper Site. The Upper Site is the uppermost site of Godhelp's Hill (see Archer *et al.* 1994a). It is well defined laterally, 3.5m in diameter, 0.5-1m in height and roughly lens-shaped in cross section (Archer *et al.* 1989). In horizontal view, the deposit would appear oval, suboval or arcuate (Archer, *pers. comm.*). The bone-rich deposits grade laterally into depauperate limestones, although the macroscopic lithological boundary is unclear. The lower levels of the assemblage contain large intra-formational clasts or masses of yellowish-white limestone. These sediments grade into a more homogenous, silty limestone. More complete vertebrate specimens are collected from the lower level.

The palaeoenvironment of the Upper Site is interpreted as a shallow (~1m) lime-rich pool in a rainforest (Archer *et al.* 1994a). Levels of calcium carbonate within the pool

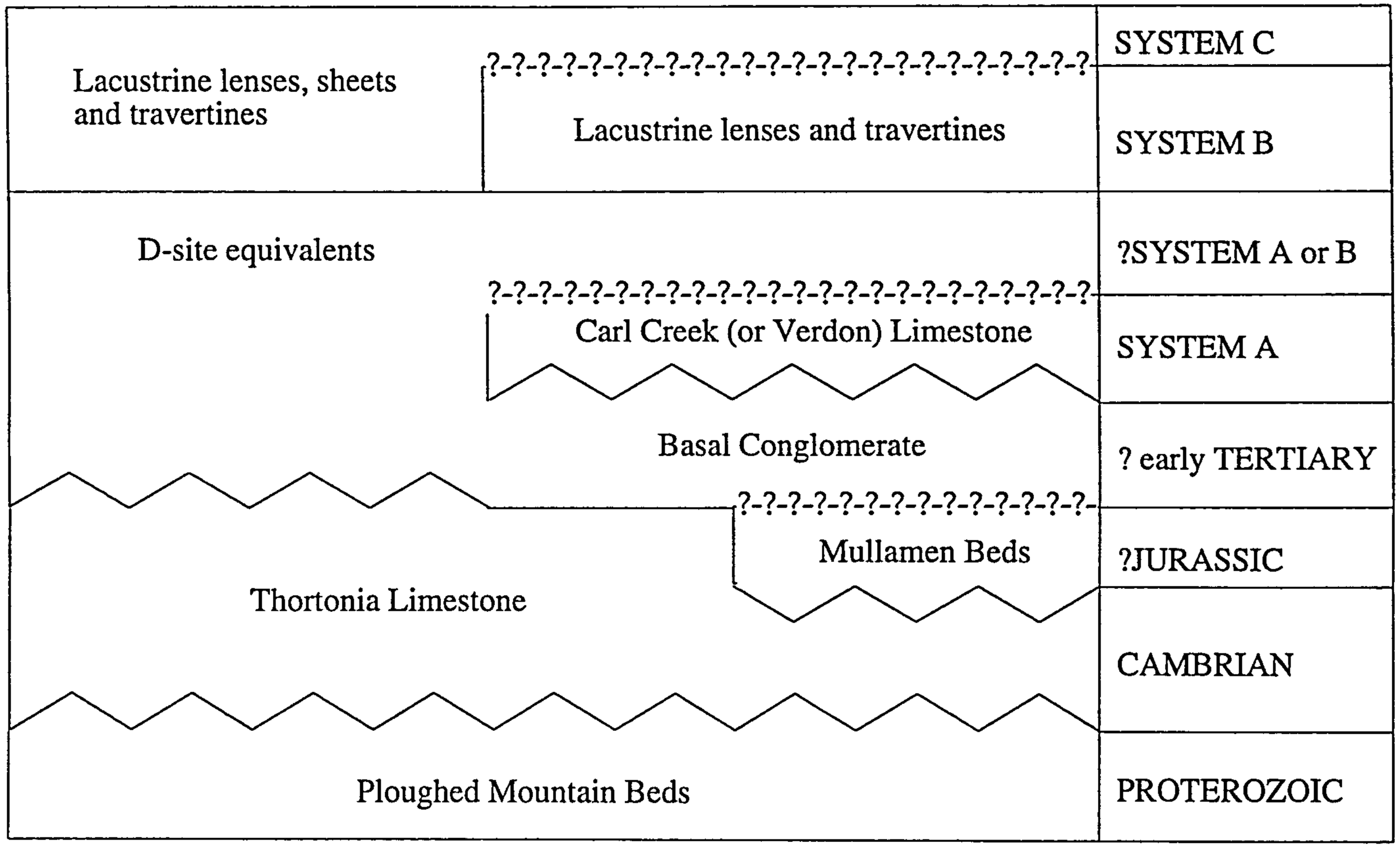


Figure 7.02 Composite stratigraphic column of the Riversleigh region. Zig-zag line indicates uncomformity. System A = Late Oligocene - Early Miocene; System B = Early - Middle Miocene; System C = Middle - Late Miocene. The Upper Site is located in the lacustrine lenses of System B. (After Archer *et al.* 1989).

are thought to have been sufficient to precipitate a thin peripheral crust, which may have appeared firm while remaining fragile (Archer *et al.* 1994a). These crusts may have been augmented by floating mats of calcium carbonate-secreting algae (Archer *et al.* 1989). Animals that strayed onto this crust would have tumbled through and drowned. Evidence in the form of accumulated piles of crystalline shards interspersed with animal remains, common in many of the Riversleigh deposits, support this theory (M. Archer *pers. comm.*).

The site is characterised by limestone with black, iron-rich bands that may reflect periodic anaerobic conditions, which would have inhibited scavengers and contributed to the lack of disarticulation of the vertebrate remains. Mineralized, wrinkled sheets, interpreted as algal mats, have also been recovered from the acid residue (Archer *et al.* 1994a), and may have further inhibited oxygenation (see Seilacher *et al.* 1985).

The vertebrate fauna is particularly diverse. It includes representatives of almost twice the number of marsupial species of any surviving Australian ecosystem, as well as a diverse range of birds, reptiles and amphibians, which sample all the surrounding micro-environments, from tree tops (many possums) to the forest floor (wynyariids, macropopoids, perameloids, etc.) and the water itself (frogs) (Archer *et al.* 1989, 1994a).

The arthropods are protected within 'egg-shell'-like concretions, which are lost during the recovery technique (Archer, *pers. comm.*). This incipient mineralization may be in some part responsible for the exceptional three-dimensional preservation.

7.2.2.4 Other sites. Besides the Upper Site of Riversleigh, insects are recovered from the Dunsinane Site, Creaser's Ramparts (D.A. Arena *pers. comm.*) and Camel Sputum (Duncan *et al.* 1997). Phosphatised nodules preserving three-dimensional plant and invertebrate material are recovered from the lacustrine sediments of the Dunsinane Site. The nodules, some of which exceed fifteen centimetres in diameter preserve specimens by replication in iron oxide-rich fluorapatite (D.A. Arena *pers. comm.*). The diverse assemblage includes wood fragments, twigs, leaves, stems, fruits, seeds, pollen, arthropods, gastropods and coprolites. The arthropod specimens, in various degrees of articulation, display a remarkable fidelity of preservation, with even internal organs occasionally preserved. Organic remains include cuticle fragments and trichopteran wing scales (<1mm).

The composition of plant organs is characteristic of a proximal assemblage accumulated by limited lateral wind transport (Collinson 1983; Spicer 1989). The presence of three-dimensional leaves and intact spongy mesophyll tissue characterise the earlier stages of leaf degradation that begins immediately after immersion or contact with the ground (Ferguson 1985; Spicer 1989). Rapid mineralisation is indicated by the prevalence of well-preserved organic material including pollen, and the exceptional external and internal preservation of mammalian coprolites particularly prone to rapid degradation (Lucas and Prévôt 1991).

7.2.3 Insect biota

The insect fauna of the Upper Site at Riversleigh is limited in terms of both abundance and diversity. It comprises five species of Coleoptera (Plate 7.7), and a trichopteran larvae (Plate 7.8) (Table 7.1; Appendix 4). The brief insect catalogue of Peter A. Jell included in Archer *et al.* (1989) is inaccurate in several places. Examination of Jell's material failed to reveal the two genera of ants (Hymenoptera: Formicidae) he observed. Similarly no cicadas (Hemiptera: Cicadidae) were found. Jell's single genera of Curculionid larvae, are in fact the larvae of Trichoptera. The other arthropods reported from the site are a myriapod (Table 7.1; Appendix 4) and an isopod (Archer *et al.* 1994a).

Each species of Coleoptera is represented by at most two specimens. Two species, represented by only a single specimen are all but complete, lacking only legs (Table 7.1). The others are incomplete, with only the head and thorax, or thorax alone, represented. The biota includes a single disarticulated elytron but its features are not taxonomically diagnostic. The most commonly recovered insect is the trichopteran larvae (n=22). No complete specimen is recovered, but fragments of each part of the organism are recovered as disarticulated fragments.

In general, the most commonly recovered insect fossils from other lagerstätten are the elytra of beetles (see Chapter 5). It is therefore striking that the Riversleigh biota is dominated by the components of the insect fauna rarely preserved elsewhere, namely the bodies of beetles (not the elytra) and larvae. While the composition of the biota may be influenced by the recovery technique (see above) it is still curious that the components which most often survive this procedure are the specimens which are rare elsewhere.

7.2.4 Fossil preservation

7.2.4.1 Material and methods. The insect specimens recovered from the Upper Site, Riversleigh were deposited with Peter A. Jell of the Queensland Museum, Australia. A representative sample of these specimens (n=37) was selected by Derek E.G. Briggs, and permission secured for appropriate sample preparation of 23 specimens (Table 7.1). Permission was also granted for destructive electron probe analysis of two specimens.

Scanning electron microscopy (Appendix A1.1). Of the original sample, 21 specimens were examined under the Scanning Electron Microscope. Each specimen was mounted on a carbon tab to facilitate removal and documentation of the underside. The specimens were gold coated.

Electron microprobe (Appendix A1.2). Thin sections of two specimens (both trichopteran larvae) were prepared for analysis under the electron microprobe. In order to ascertain the mineralogy of the specimens a full suite of elements was sought (F, Na, Mg, Al, Si, P, S, K, Ca, Ti, Cr, Mn, Fe, and Ni). A single traverse across the body cavity of each was conducted in order to establish changes in chemistry from periphery to core.

TAXA	ACCESSION NO.	DESCRIPTION	SIZE	PLATE
COLEOPTERA				
Curculionidae				
Species A	QMF34585	damaged head/thorax	5mm	
	QMF16648	head/thorax	6	7.5A, I; 7.7.A
Species B	QMF34583	head/thorax	5	7.5B-D, K; 7.7B
	QMF34586	thorax	3	
?Histeridae	QMF34582	beetle without legs	5	7.3A-B; 7.5G,J; 7.7C
Archostomata	QMF34595	beetle without legs	7	7.6D; 7.7D; 7.8A-C
TRICHOPTERA				
Species A	QMF34584	head/thorax/abdomen	7	7.5F,H; 7.6A, B
	QMF34593	head/thorax/abdomen	8	7.9B
	QMF34587	thorax	4	7.2A-F; 7.9A
	QMF34588	thorax/abdomen	6	
	QMF34589	single segment	2	
	QMF34590	single segment	2	
	QMF34592	tail assembly	4	7.1C-D; 7.6C
	QMF34594	tail assembly	3	7.9C, D
	QMF34591	tail assembly	3	7.4A-B
	Specimens A	tail assembly	3	
	Specimens B	tail assembly	3	
MYRIAPODA				
Species A	QMF34596	thoracic segments	4	

Table 7.1 The Riversleigh (Upper Site) insect fauna upon which SEM was conducted. Microprobe analysis was conducted upon specimens in *italics*.

7.2.4.2 Mineralogy and preservation. Electron microprobe analysis of the specimens indicated the presence of calcium, phosphorus and fluorine in the proportions indicative of carbonate-fluor-apatite (CARFAP) (Fig. 7.03). Specimen A reveals zones of CARFAP absence corresponding with voids in the specimen. A significant proportion of Si is revealed in one such void. This presumably represents a grain of silica, since no other element is found in significant proportions.

While some of the specimens are hollow most have an infilling of detrital material. This material is also composed of CARFAP (Fig 7.03). Although individual layers are preserved, there is no variation in mineralogy.

Conditions under which decay and mineralization take place have been shown to vary on a sub-millimetre scale within a decaying carcass (Martill 1988; Briggs and Kear 1994). The influence of different micro-environments (of either decay or indeed diagenesis) is evident on a micron scale within the Riversleigh insects. The cuticle of a trichopteran larva may display distinct chevron structures arranged in parallel rows just a few microns (Plate 7.1B) from a point where it has been replaced by plates of phosphate which replicate the gross structure but obliterate the detail (Plate 7.1A). A similar phenomenon is evident where the nodular patterning of the larval cuticle (Plate 7.1D) is replaced within a few microns by plates of phosphate (Plate 7.1C).

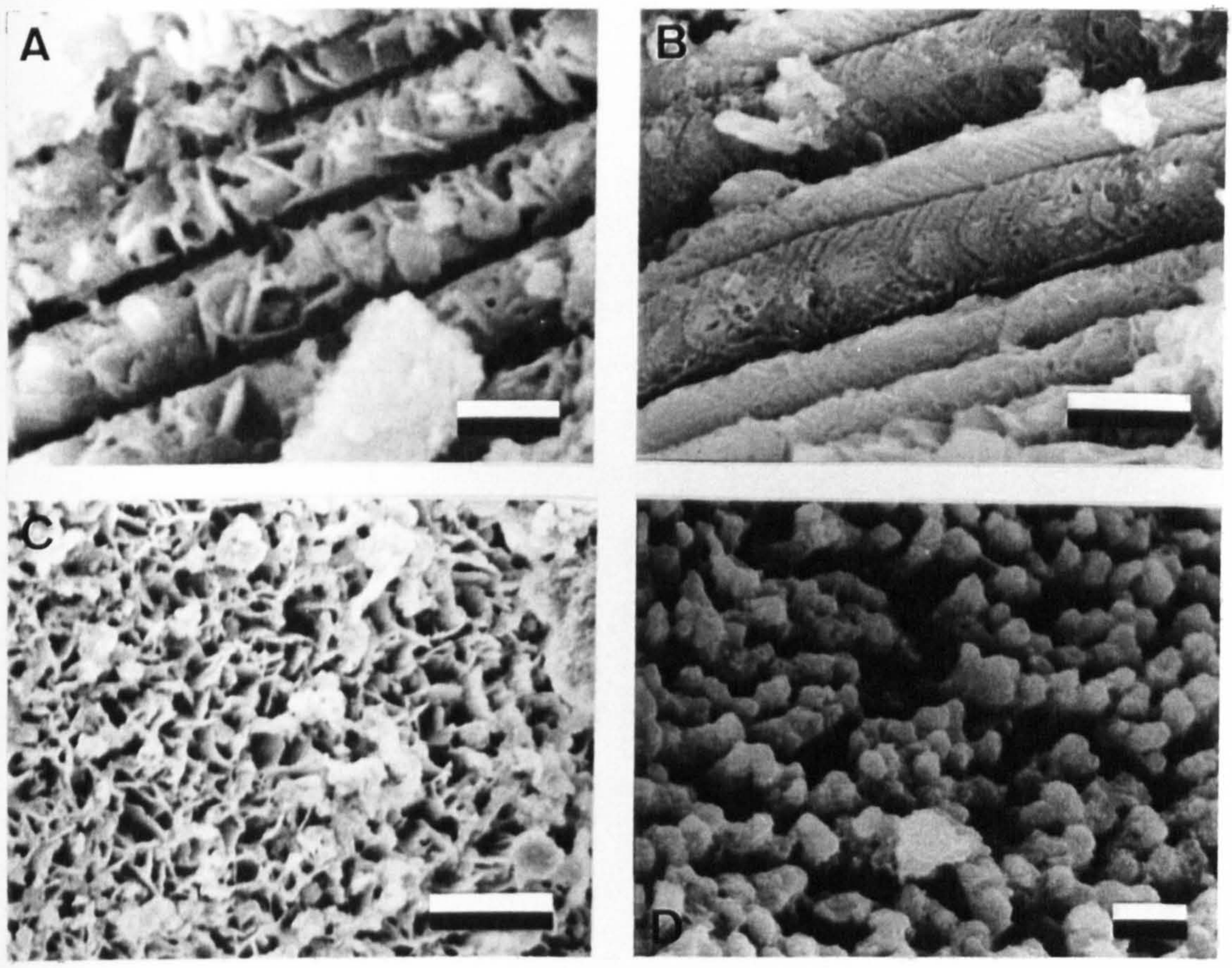
7.2.4.3 Cuticle. Structures less than 1μm in dimension are preserved on the cuticle surface (Plate 7.3). Where exposed, the interior retains a distinct lineation (Plate 7.2, 7.4C). In cross section the helicoidal structure observed by Bouligand (1965) and Neville *et al.* (1969) in living insects is evident, here displayed in the trichopteran larva (Plate 7.2D). The crystalline orientation follows the original orientation of the structural proteins and other biomolecules within the cuticle, providing further evidence for the fidelity of replication by calcium phosphate. Parallel canals can be discerned within the tail segment of one of the larvae (Plate 7.2C).

7.2.4.4 Eye. The fidelity of preservation displayed in the eyes is also striking (Plate 7.5). The compound eye of insects is composed of arrays of ommatidia - the basic visual unit (Snodgrass 1935) (Plate 7.5F). Each ommatidium is composed of a dioptric apparatus and rhabdom, isolated from the next ommatidium by pigment cells; the dioptric apparatus of lens and crystalline cone control the focusing of light. The cuticle of this apparatus is composed of chitin which differs ultrastructurally from the chitin surrounding it (Neville 1970). The rhabdom contains the visual pigments which trigger impulses in the optic nerve (Snodgrass 1935). As a result of replication in calcium phosphate the Riversleigh specimens preserve the entire ocular apparatus.

The specimens exhibit varying degrees of post-mortem and post-diagenetic damage to the eye. Where the lenses (diameter 30μm) are preserved, the characteristic hexagonal-packing arrangement of the compound eye is apparent (Plate 7.5A, I). With the deflation

Plate 7.1 Micro-environments of preservation (QM F34592). A, cuticular fragment from within the tail assemblage of the larva displaying distinct chevron structures arranged in parallel rows; x 65,000. Structural detail is lost to the lower right. B, Cuticle of larva a few microns distant to 'A'; x 65,000. The structures have been replicated by plates of calcium phosphate such that the gross structure is retained while the detail is lost. C, 'nodular' surface of the dorsal cuticle of the larva; x 25,000. D, replacement of the nodules within a few microns of 'C' with plates of calcium phosphate; x 30,000. Specimens gold coated.

Plate 7.2 Underlying arrangement of microfibrils and canals within the cuticle of coleopteran (A, B; QM F34582) and trichopteran larva (C, D; QM F34591). A, longitudinal arrangement of microfibrils; x 13,000. B, longitudinal and cross-sectional arrangement of microfibrils; x 32,500. C, series of parallel canals exposed in tail segment; x 9,000. D, helicoidal pore canals (*cf.* Bouligand 1965) in a cuticle fragment; x 27,500.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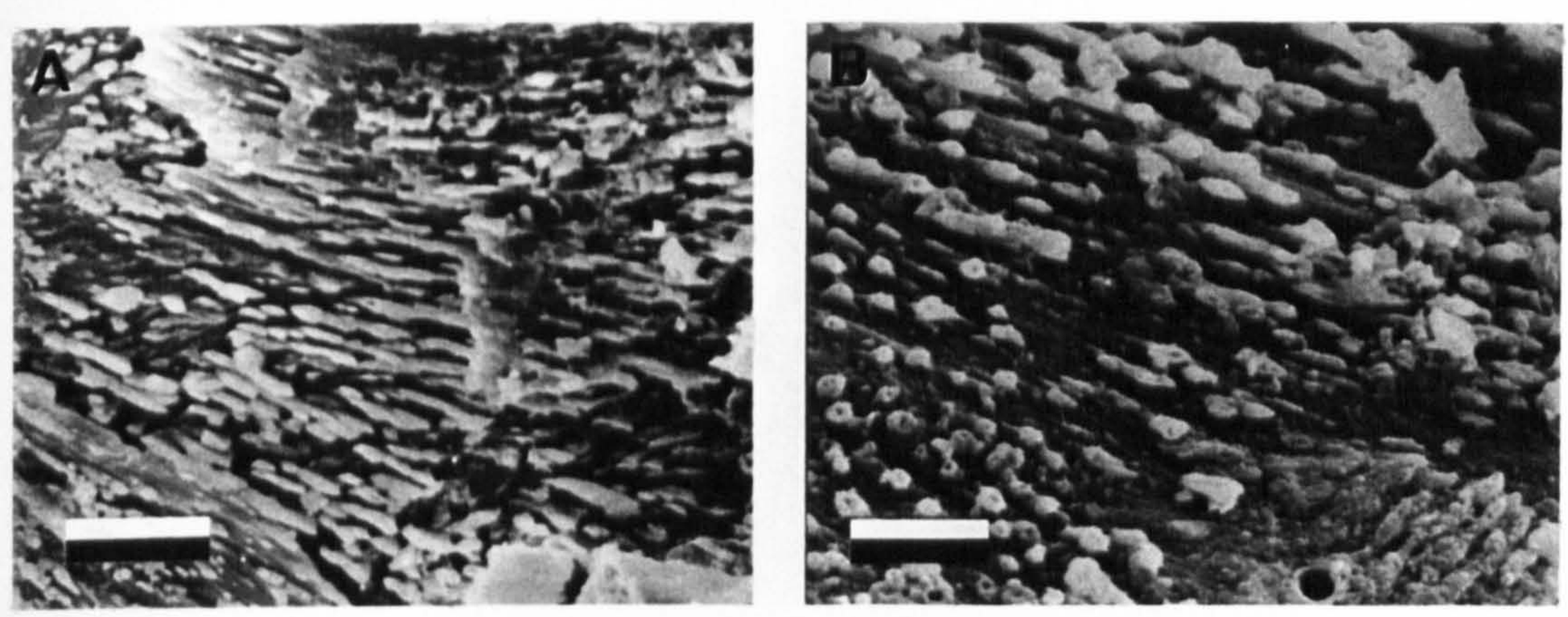
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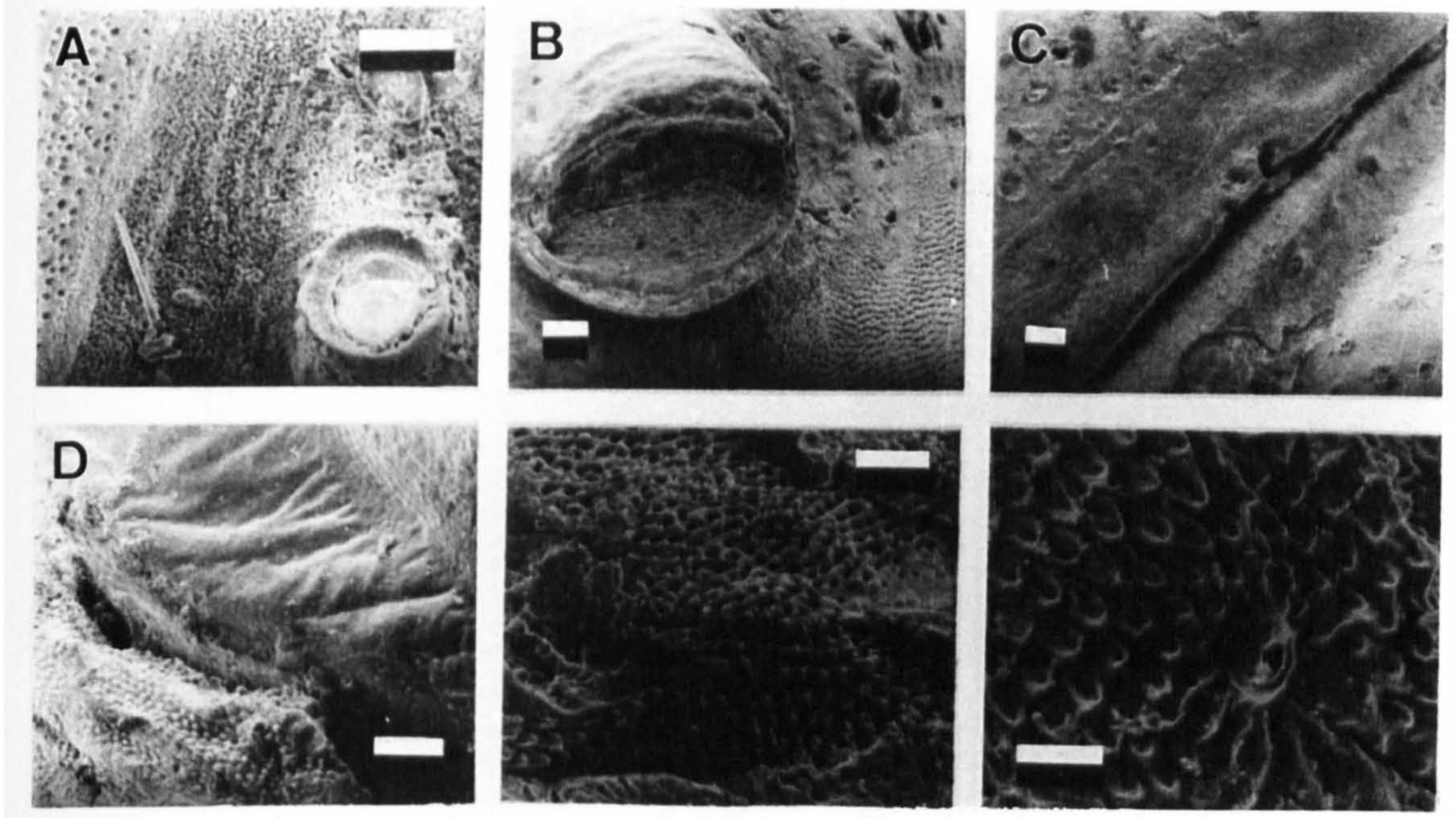
Plate 7.3 Ornamentation of cuticle of trichopteran larva (QM F34587). A, prescutum with irregular pattern of pits; x 4,500. A spiracle is also present. B, interface between the scutum, showing sites of hair emplacement in its upper half, and the scutellum; x 5,000. The scutellum is more regularly patterned than the prescutum. C, scutum and scutellum, overlapping the next segment (to the right); x 4,000. D, limb of first thoracic segment, surrounded by arthrodial membrane; x 700. E, arthrodial membrane; x 1,750. F, close up of hair emplacement; x 2,250.

Plate 7.4 Cuticle and wing of ommatid (Coleoptera) (QM F34595). A, break in cuticle reveals distinct alignment of microfibrils; x 9,000. B, terrace-like pattern of cuticle between wings on ventral surface; x 6,000. C, close up of wing; x 6,000.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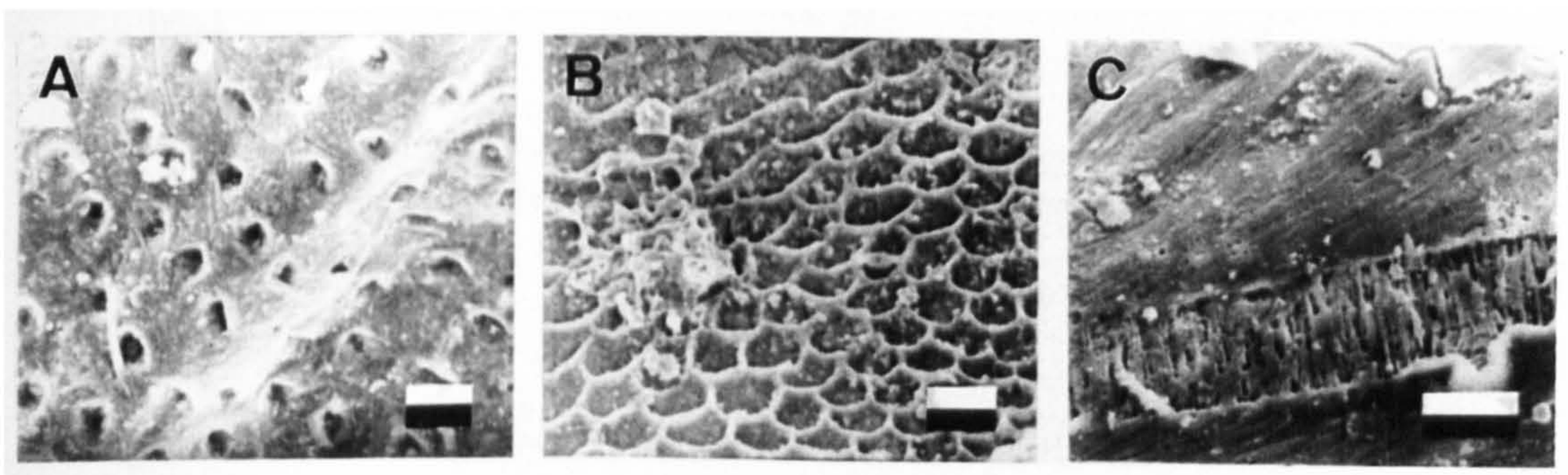
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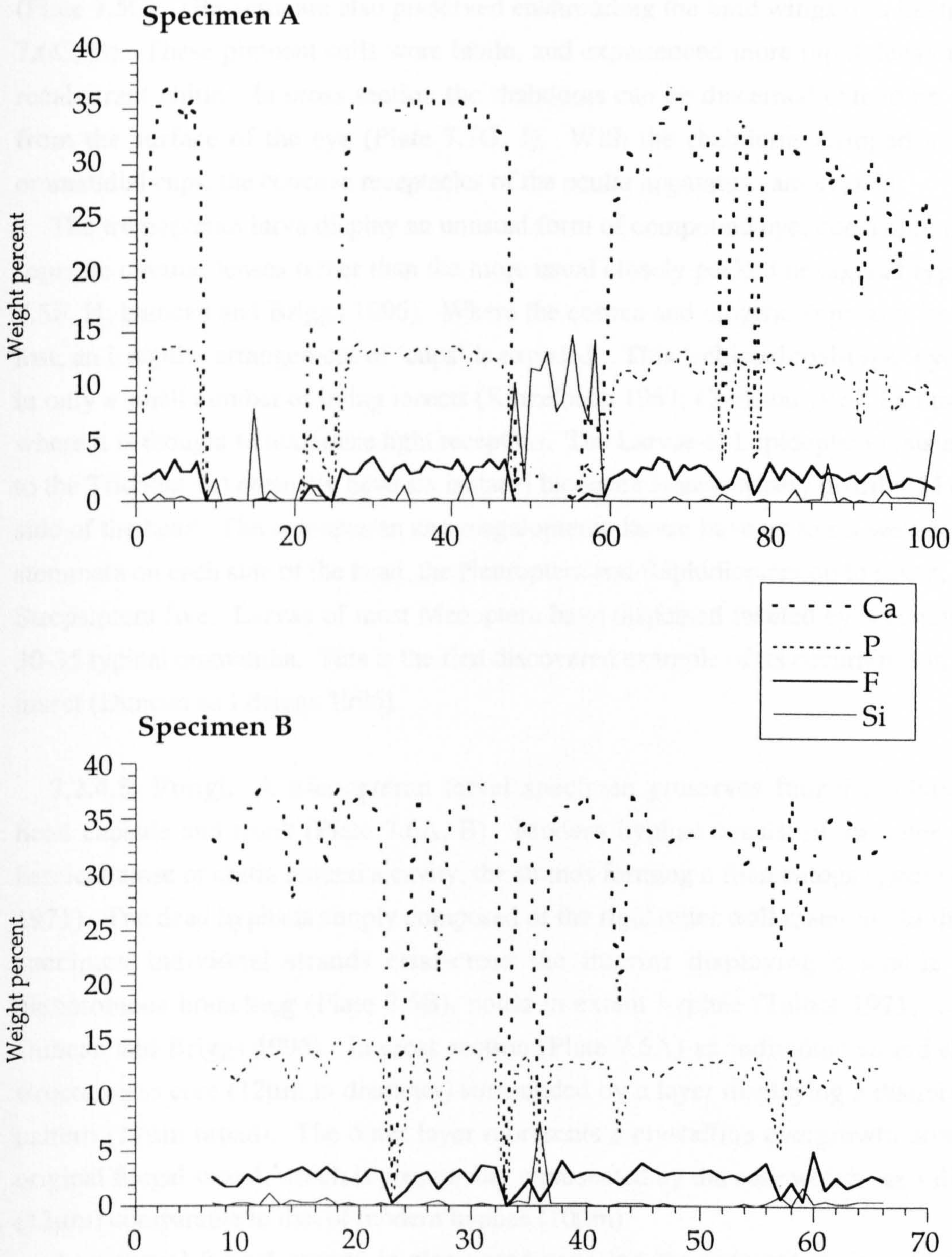

Figure 7.03 Microprobe traverse across two specimens.

of an individual lens through decay, crystal aggregates are evident in the interior. Where the dioptric apparatus is lost, the rhabdom emplacement is exposed (Plate 7.5B, D, K). The pigment cells that once lined the rhabdom interior of one specimen have been destroyed by bacteria, which are now preserved as rod-like protuberances from the walls (Plate 7.5C). (Bacteria are also preserved enshrouding the hind wings of a beetle: Plate 7.6C, D). These pigment cells were labile, and experienced more rapid decay than the recalcitrant chitin. In cross section the rhabdoms can be discerned extending radially from the surface of the eye (Plate 7.5G, J). With the rhabdoms stripped away, the ommatidial cups, the concave receptacles of the ocular apparatus, are evident.

The trichopteran larva display an unusual form of compound eye, consisting of large, separate circular lenses rather than the more usual closely packed hexagonal type (Plate 7.5F, H; Duncan and Briggs 1996). Where the cornea and dioptric apparatus have been lost, an irregular arrangement of 'cups' is exposed. This 'schizochroal-type' eye occurs in only a small number of living insects (Kinzelbach 1967; Clarkson 1979; Paulus 1979), where it is thought to maximise light reception. The Larvae of Lepidopteran (sister group to the Trichoptera) normally have six isolated biconvex lenses, widely distributed on each side of the head. The coleopteran and megalopteran larvae have up to six well-separated stemmata on each side of the head, the Neuroptera and Raphidioptera up to seven, and the Strepsiptera five. Larvae of most Mecoptera have dispersed faceted eyes consisting of 30-35 typical ommatidia. This is the first discovered example of its occurrence in a fossil insect (Duncan and Briggs 1996).

7.2.4.5 Fungi. A trichopteran larval specimen preserves fungal hyphae in the head capsule and trunk (Plate 7.6A, B). Modern hyphae consist of an outer wall of hemicellulose or chitin around a cavity, the strands forming a filamentous system (Talbot 1971). The dead hypha is simply composed of the rigid outer wall material. In the fossil specimen individual strands criss-cross the interior displaying a simple lateral dichotomous branching (Plate 7.6B), noted in extant hyphae (Talbot 1971; see also Duncan and Briggs 1996). In cross section (Plate 7.6A) an individual strand shows a structureless core (12μm in diameter) surrounded by a layer displaying a distinct radial pattern (17μm broad). The outer layer represents a crystalline overgrowth around the original fungal strand, which is presumably represented by the core which has a diameter (12μm) comparable to that of modern hyphae (10μm).

An unusual fungal growth is also noted covering the external surface of a larval segment, where a number of strands appear to radiate from a central point each joined by short lengths to form a distinctive meshwork (Plate 7.6D).

7.2.5 Discussion

Early-diagenetic phosphate is now recognized as perhaps the most important early authigenic mineral in soft-tissue preservation, frequently replicating soft tissue at a

Plate 7.5 Compound eyes. A, lenses displaying characteristic hexagonal packing (QM F16648); x 2,500. B, framework of pigment cells revealed by loss of dioptric apparatus (QM F34583); x 7,000. C, walls of rhabdomal emplacement lined with bacteria (QM F34583); x 20,000. D, framework of the eye (QM F34583); x 1,500. E, schematic of ommatidium of apposition eye. Abbreviations: C, corneal lens; CC, crystalline cone; PYPC, primary pigment cells; SPC, secondary pigment cells; RC, retinal cells; R, rhabdom. F, 'Schizochroal-type' eye of trichopteran larva (QM F34584); x 2,750. G, cross-section through rhabdomal emplacement showing ommatidial cups (QM F34582); x2,000. H, close up of 'schizochroal-type' eye, showing ommatidial cups (QM F34584); x2,750. I, complete eye (QMF 16648); x 720. J, complete eye (QM F34582); x 2,500. K, complete eye (QM F34583); x 480.

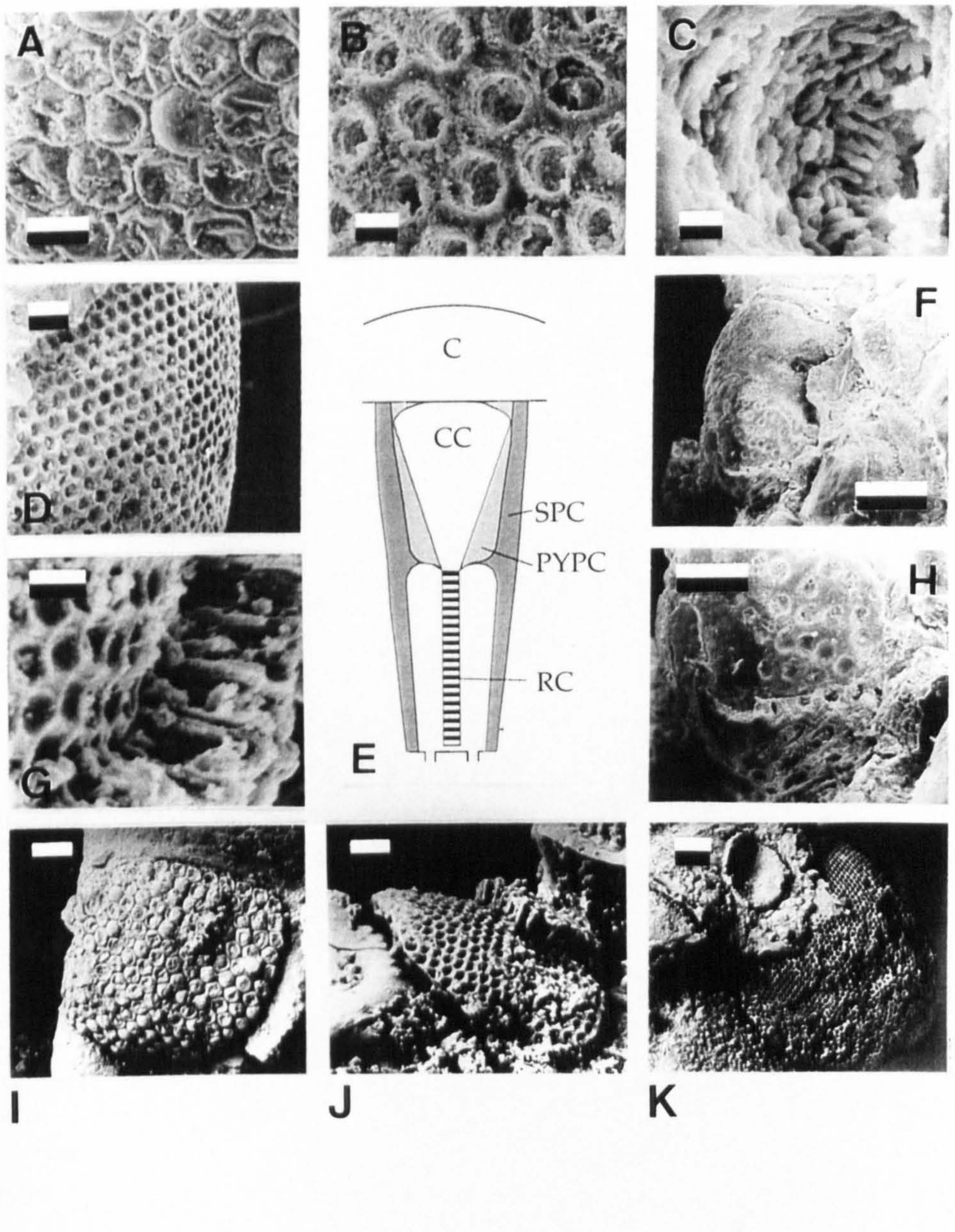
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Plate 7.6. Fossil fungi and bacteria. A, fungal hyphae criss-crossing the interior of head and thorax of larva (QM F34584); x 1,750. B, cross-section through single fungal strand (QM F34584); x 9,000. C, fungal colony covering sternite of larva (QM F34592); x 225,000. D, bacterial mat covering surface of coleopteran wing (QM F34595); x 600.

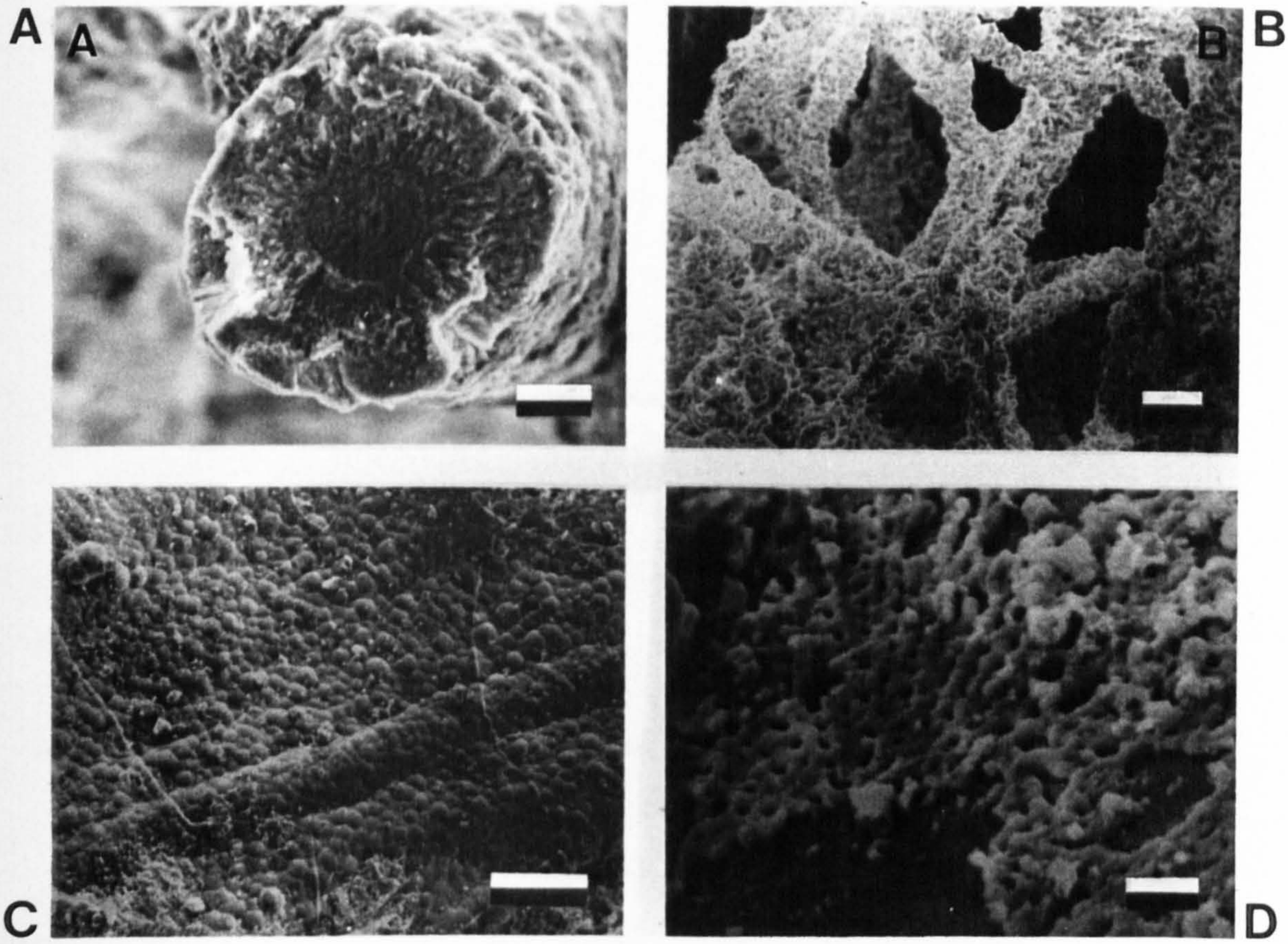
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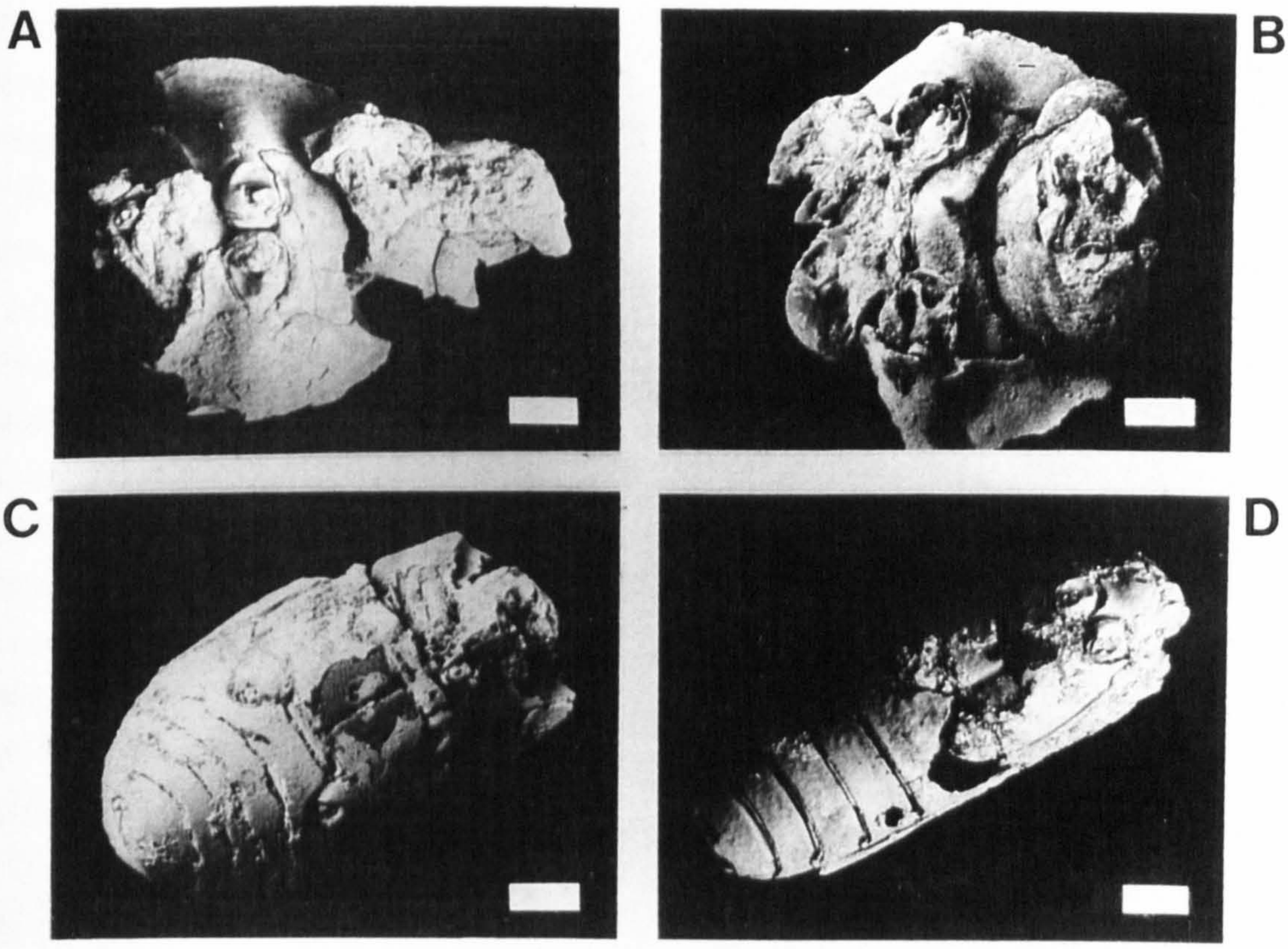
Plate 7.7. Coleoptera. A, undetermined curculionid (QM F16648); x 100. B, undetermined polyphagan (QM F34583); x 120. C, undetermined histerid (QM F34582); x 120. D, undetermined ommatid (QM F34595); x 60.

Plate 7.8 Trichopteran larva. A, composite image of head, thorax and upper abdomen (QM F34587); x 80. B, ventral view of head (QM F34593); x 100. C,D, tail assemblage (QM F34594); x 140.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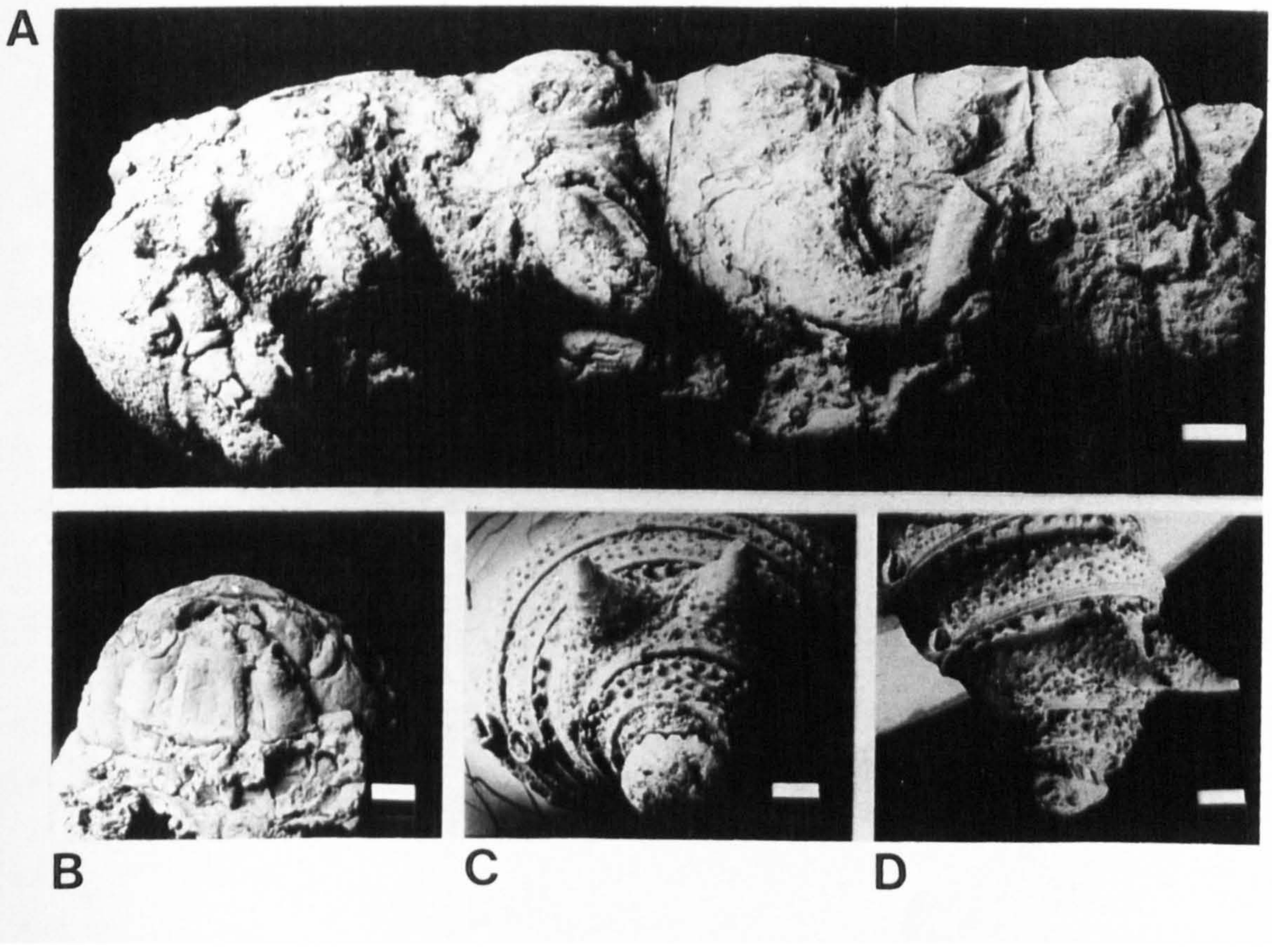
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resolution of microns (see Martill 1988, 1989; Schultze 1989; Wilby 1993; Briggs *et al.* 1993; Martill and Wilby 1994; Wilby and Whyte 1995; Wilby *et al.* 1995). The process of phosphatization has recently been induced successfully in the laboratory under controlled conditions (Briggs and Kear 1993b, 1994b).

Tissues relatively high in organic phosphorous (Balson 1980; Allison 1988a, b) are particularly susceptible to phosphatisation under conditions of high microbial activity (Lucas and Prévôt 1991; Allison 1988a, b; Briggs and Kear 1993b; Briggs *et al.* 1993). Preservation may be further enhanced under 'closed' conditions, *e.g.* by microbial mats (Seilacher *et al.* 1985; Briggs *et al.* 1993; Wilby and Martill 1992). Soft-tissue may also be pseudomorphed by phosphatized microbes (*e.g.* Willems and Wuttke 1987; Micklich and Wuttke 1988; Clark 1989; Mehl 1990; Martill and Wilby 1993a). The microbes generally infest only the peripheral tissue of the carcass where access to the external environment is unimpeded (*e.g.* skin, gills or rhabdomal emplacement), or are associated with typically bacteria-rich tissues and organic material (*e.g.* alimentary tract and faeces). The microbes typically preserve a very smooth external surface suggesting that mineral deposition occured within a membrane-bound space.

By comparison of fossil material and the products of decay it has been inferred that phosphatisation of fresh tissue can take place over a time period as short as a few hours (*e.g.* Martill 1988; Martill and Harper 1990). However, laboratory experiments utilizing phosphate-rich soft tissue have achieved mineralization only over a period of several weeks and have yielded only limited mineralised tissue (Briggs and Kear 1993b, 1994b; Briggs *et al.* 1993). Even under ideal conditions, mineralisation is often selective or patchy (Müller 1985; Martill 1988; Wilby and Martill 1992; Briggs and Kear 1993b; Briggs *et al.* 1993).

As noted, the phosphatized insects of the Upper Site of Riversleigh display remarkable cuticular preservation. However, preserved internal soft tissue is almost entirely absent, except where preserved as small fragments within the detrital infilling of some specimens. Therefore the insects of Riversleigh must have undergone protracted soft-tissue decay before the onset of mineralization. The delicate fungal strands that criss-cross the interior of certain carcasses suggests that they remained hollow long enough for fungal growth to reach an advanced state. The experiments of Chapter 2 indicate that insect soft-tissue, at a temperature of 25°C, were generally consumed within a matter of weeks (although small residual fragments of tissue still remain). The remaining hollow cuticle sac persisted for considerable periods of time (see Fig. 2.09, Chapter 2), and was occasionally colonised by fungi.

The bacteria noted within the peripheral, rhabdomal tissue of a beetle specimen, while certainly responsible for the consumption of soft-tissue need not be directly implicated in cuticle preservation. However, the bacteria may be responsible for liberating sufficient phosphate ions to initiate the mineralization process (see Willems and Wuttke 1987; Micklich and Wuttke 1988; Martill and Wilby 1993a).

Besides the Upper Site, early-diagenetic phosphatisation occurs in other Riversleigh fossil deposits, *e.g.* Dunsinane Site, Creaser's Ramparts (D.A. Arena *pers. comm.*). The phosphatized Dunsinane nodules preserve tissues generally regarded as low in organic phosphorus, particularly plant material (D.A. Arena *pers. comm.*).

The exceptional preservation of soft tissue in the Riversleigh insects raises several questions regarding both the rate and mechanism of mineralization. Most models for exceptional preservation require rapid burial, anoxicity, or both in order to preclude scavenging and bacterial decay (Seilacher *et al.* 1985). In the case of Riversleigh only the more recalcitrant tissue (*i.e.* chitin/protein complex, or calcified chitin in the case of the myriapod) is preserved. This, coupled with the presence of bacteria within the rhabdom emplacements and fungal hyphae in the head capsule of one of the specimens, suggests that decay proceeded for some time prior to mineralization, and that during this period the carcass was undisturbed.

Phosphatisation may be the result of a rare convergence of limiting parameters, notably phosphate availability, pH and temperature. Phosphate may originate in the surrounding skeletal bone material, or the rotting flesh of the vertebrate carcasses. The partially phosphatised bone de-mineralised by prevailing acidity, in a process similar to that which affects bone in highly acidic sediments such as peat, would free phosphate ions (Connolly 1986), as would the general breakdown of flesh.

Briggs and Kear (1993b, 1994b) considered pH to be the main control of mineralization. Under closed conditions, a decrease in pH was considered to inhibit the precipitation of calcium carbonate and favour that of calcium phosphate (see Briggs and Wilby 1996). Algal mats (Archer *et al.* 1989) may have played a crucial role in closing the Riversleigh system (see also Seilacher *et al.* 1985) and depressing pH. The trichopteran larvae, recovered from tube-like extensions within the algal mats may have exprienced a micro-environment of preservation. It could be argued that the limited insect diversity is in some way connected with the relationship of insect and algal mat.

7.3 BEMBRIDGE MARL LIMESTONE

7.3.1 Introduction

The Bembridge Marls Insect Bed of the Isle of Wight (Fig. 7.04), southern England (Late Eocene; 36 Ma) is the most significant insect lagerstätten of the British Tertiary, with some 200 species recorded from twenty orders (Jarzembowski 1980). While the fossil assemblage is dominated by wings, exceptional three-dimensional insects that preserve not only calcified internal tissue, but also altered organics, occur

7.3.1.1 Previous studies. Insects from the north coast of the Isle of Wight were first reported over a century ago (A'Court Smith 1874). A'Court Smith, who discovered the fossil biota in 1859, amassed the most substantial, is somewhat biased, collection of Bembridge insects. The Rev. P.B. Brodie, an amateur palaeoentomolgist, also acquired a collection of some 2000 specimens, and published a number of general treatments (Brodie 1878, 1894a, b). Both collections were ultimately secured by the Natural History Museum (London).

The arthropod fauna has been selectively described (Smith 1879; McCook 1888; Jones and Sherborn 1889). The first insect described was a lepidopteran, *Lithopsyche antiqua* (Butler 1889). The most substantial study of the insect biota was conducted by T.D.A. Cockerell (1915-1922). However, following this flurry of publication, the biota remained untouched until recently, when E.A. Jarzembowski (1980) reviewed the fauna, revised the orders Trichoptera, Isoptera, Plecoptera, Megaloptera, Neuroptera and Mecoptera, and assessed their palaeoecological significance.

The flora of the Bembridge marls has received some attention (Reid and Chandler 1926; Collinson 1983), and a number of general treatments of the palaeoenvironment have been published (Daley 1969, 1972, 1973; Hooker *et al.* 1995; Armenteros *et al.* 1997).

7.3.1.2 Material and localities. The most extensive collection of Bembridge insects is the A'Court Smith/Brodie collection held by the Natural History Museum (London), with some 9000 specimens. However it is considerably biased, as A'Court Smith discarded over half the fossils recovered because of 'perverse fracture'. Minor collections are held by a number of institutions, including the Smithsonian Institution, Washington D.C. and the Geology Museum of the Isle of Wight at Sandown. However, the Mitchell collection of the Maidstone Museum and Art Gallery (England), amassed in Thorness Bay during a single field seasont, includes all the fossils recovered and is therefore the least affected by collection bias.

Most of the specimens of A'Court Smith and Brodie were collected from Gurnard Ledge of east Thorness Bay (Jarzembowski 1980) (Fig. 7.04). Insects have also been recovered from to the west in an exposure stretching some 500m west of Burnt Wood

(Fig 7.04). The Thorness Bay sites along the north-west coast are the richest of the localities. Plant fragments are the most frequently recovered fossils. Insects, both small wings and 3D articulated specimens preserving organic cuticle and internal mineralizaed tissue, are comparatively rare.

On the north-east coast insects have been reported from a 300m long outcrop at Node's Point (Fig. 7.04), just above the cliff base, and from cobbles which litter the foreshore south-east of the town of Bembridge. Neither site has recently yielded insects. The insect-bearing horizon also occurs in the lower cliff face of the neighbouring Whitecliff Bay (Fig. 7.04) but no insects have been reported.

Conchoidal fracturing of the insect-bearing limestone creates random cross-sections through insect bodies making identification problematic. Determination, even to ordinal level, is possible only where an obvious diagnostic feature is visible (such as wings, or the hymenopteran 'waist'). Although the Mitchell collection provides a reasonably accurate representation of relative abundance, inferences based on taxonomic composition are preliminary, pending a complete systematic study.

7.3.2 Geological setting

7.3.2.1 Introduction. During the Palaeogene, the Isle of Wight formed part of the southern Hampshire-Dieppe Basin, which occupied a marginal position, with land to the west and sea to the east (Daley 1972). The Solent Group of sands, silts, clays, and occasional freshwater limestones was deposited during this time in a predominantly non-marine environment (Fig. 7.05).

The Bembridge Marls Member (Bouldnor Formation: Fig. 7.05) is an argillaceous sequence of brackish lagoonal and estuarine sediments with occasional thin sands and freshwater limestones, which accumulated during a series of short-lived transgressions in the early Tertiary (Daley 1972, 1973). The brackish lagoonal fauna is dominated by the bivalve *Polymesoda* (Jarzembowski 1980). The lower beds, including the Insect Bed, were deposited during a transgressive phase, and the remainder within a low-lying flood plain environment during the ensuing regression (Daley 1973). The entire member reaches a maximum thickness of some 34m (Daley 1972).

The outcrop of the Bembridge Marls is limited to the north-east and north-west coasts of the Isle of Wight (Fig. 7.04), where it lies unconformably on the prominent Bembridge Limestone, which is comprised of lacustrine and palustrine facies (Hooker *et al.* 1995; Armenteros *et al.* 1997). The term 'Insect Bed' refers to all lithologies between two laterally persistent, readily distinguishable shelly horizons (Jarzembowski 1980; Fig. 7.06). During the summer of 1996, the four principal insect-bearing sites were logged. The four logs are included in Appendix A2.2, with the pertinent details summarized in Fig. 7.06.

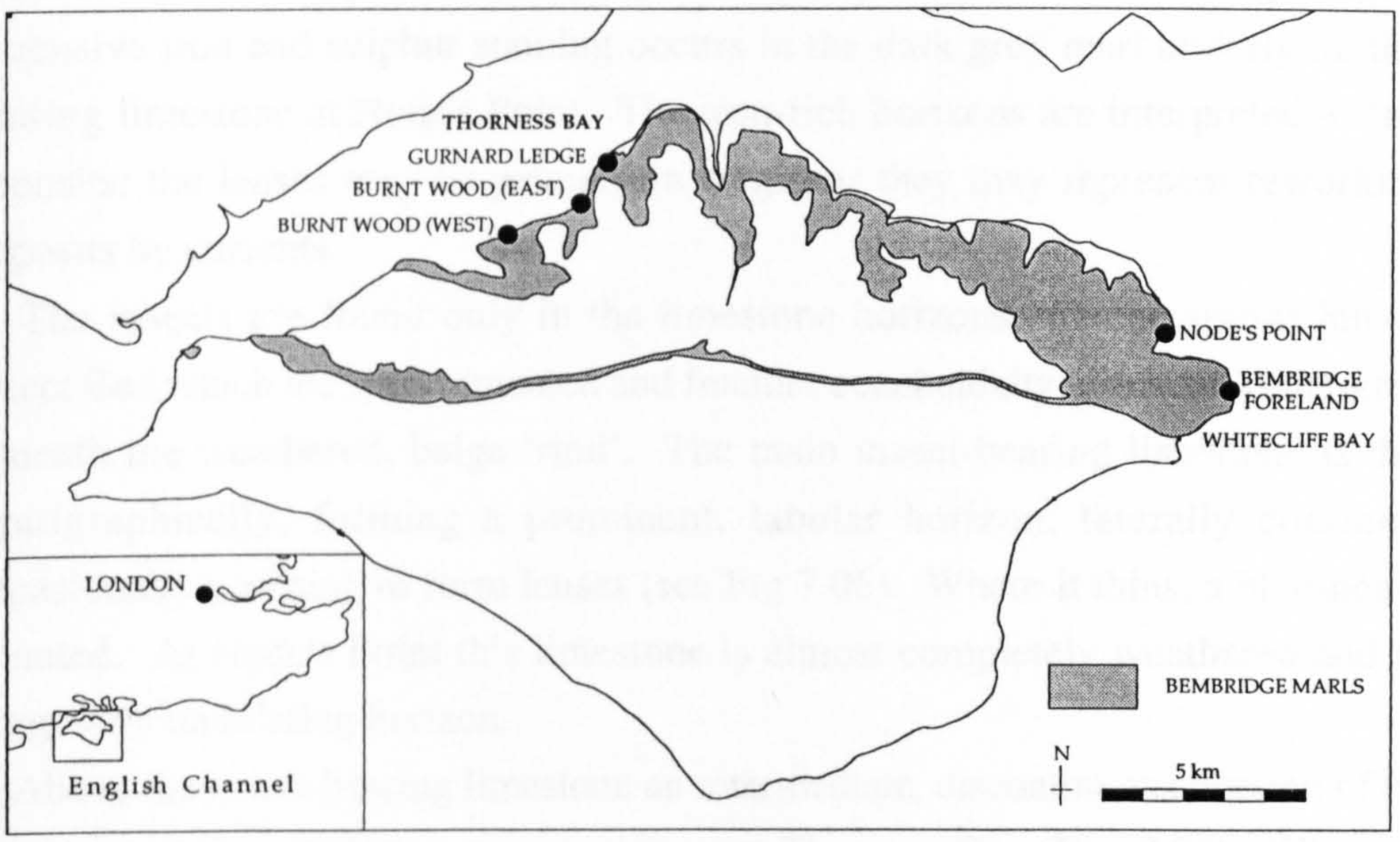


Figure 7.04 Isle of Wight, UK showing outcrop of the Bembridge Marls (Oligocene) and localities mentioned in the text. Map after Jarzembowski (1980).

7.3.2.2 Sedimentology. The Insect Bed is dominated by a dense, dark grey mudstone, often laminated and weathering light grey. At Burnt Wood, a laminated, beige mud constitutes the background lithology. Iron-rich horizons and lenses are common, particularly in the uppermost and lowermost shelly horizons demarcating the Insect Bed. Extensive iron and sulphur staining occurs in the dark grey marl underlying the insect-bearing limestone at Node's Point. The iron-rich horizons are interpreted as tuffaceous deposits: the lenses may be primary in origin or they may represent reworking of the deposits by currents.

The insects are found only in the limestone horizons and calcareous lenses of the Insect Bed which are well cemented and fracture conchoidally to reveal a blue-grey 'heart' beneath the weathered, beige 'rind'. The main insect-bearing limestone is the lowest stratigraphically, forming a prominent, tabular horizon, laterally continuous and occasionally pinching to form lenses (see Fig 7.06). Where it thins, a blue-hearted mud is noted. At Node's Point this limestone is almost completely weathered and forms an irregularly undulating horizon.

Above the insect-bearing limestone an intermediate, discontinuous horizon of limestone lenses and beige mudstone crops out in west Thorness Bay (Fig. 7.06). Where the band thins, it is traced by a beige mud. A thin, lenticular band of indurated marl is laterally equivalent to the east at Burnt Wood. At Gurnard Ledge, two discrete lenses are the only evidence of this horizon, which is absent from localities further east. An upper horizon of calcareous lenses crops out only in the western Thorness Bay area. A blue marl halo surrounds each lens. At Burnt Wood this horizon becomes a tabular band of indurated marl.

Daley (1972) interpreted the main insect-bearing limestone (Fig. 7.06) as primary, but regarded the discontinuous lenticular bands as diagenetic in origin. He supported a diagenetic interpretation with evidence that laminae within the calcareous lens continue into the adjacent mudstone. He also considered the rounded lens shape as diagnostic of concretionary growth. However, the laminations within the lenses between Gurnard Ledge/Sticelett Ledge (GR 462 942) and Burnt Wood (GR 438 929) cannot be traced into the mudstone beyond, suggesting that the lenses are primary in origin. In addition, the majority of the lenses are flat-topped, a feature consistent with their formation as channels. Only one rounded lens was discovered during the course of this study, near Burnt Wood (GR 437 927), which may suggest a secondary phase of calcareous enrichment acting upon a primary structure. Thus both primary and diagenetic processes were involved in the formation of the lenses.

7.3.2.3 Palaeoënvironment. The presence of the pulmonate *Galba*, together with insects and terrestrial plant fragments, suggests that the limestone of the Insect Bed is freshwater in origin. The abundant anostracan crustaceans (*Branchipodites vectensis*), which are often found in association with the insects, offer further evidence of fresh

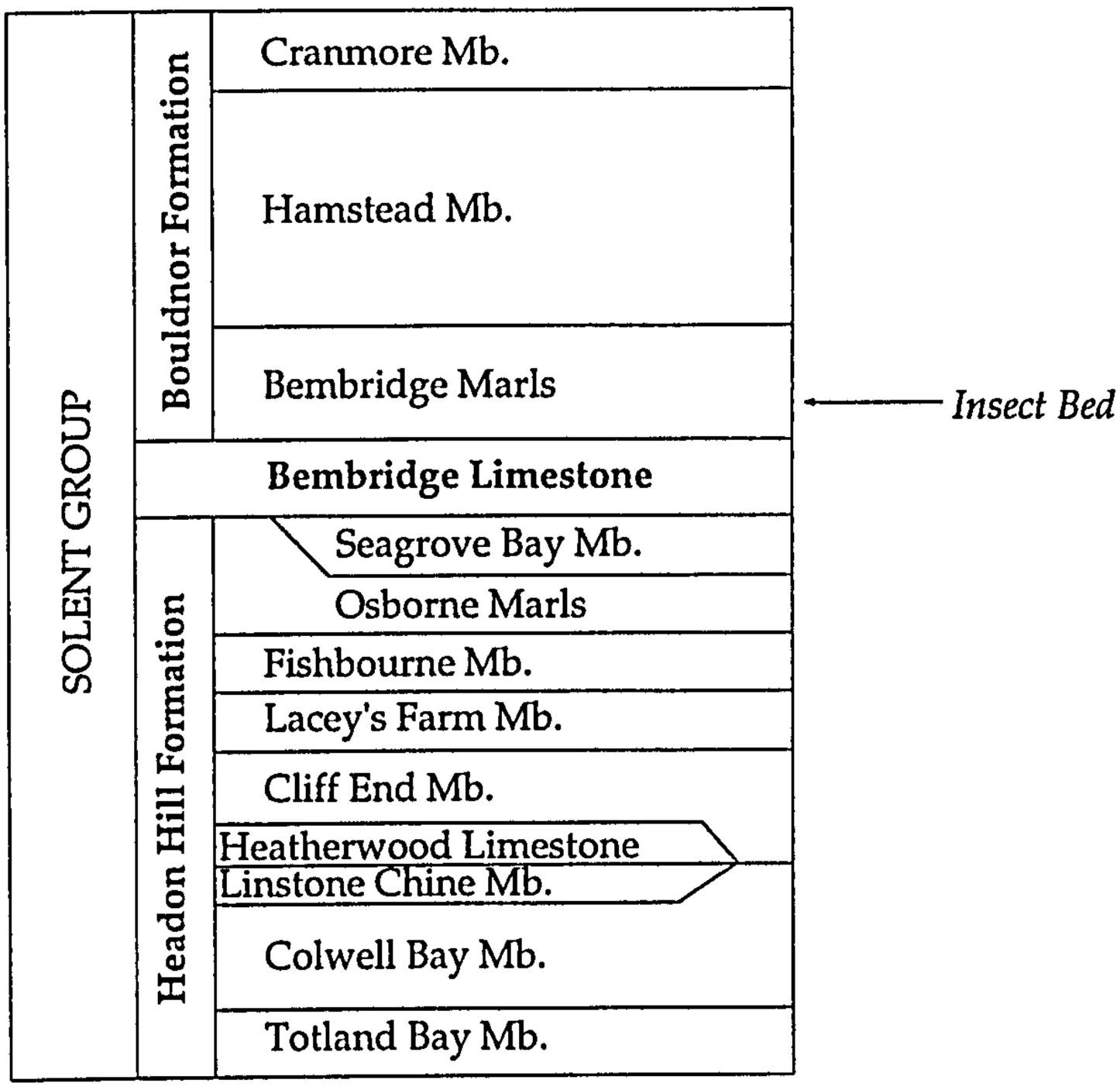
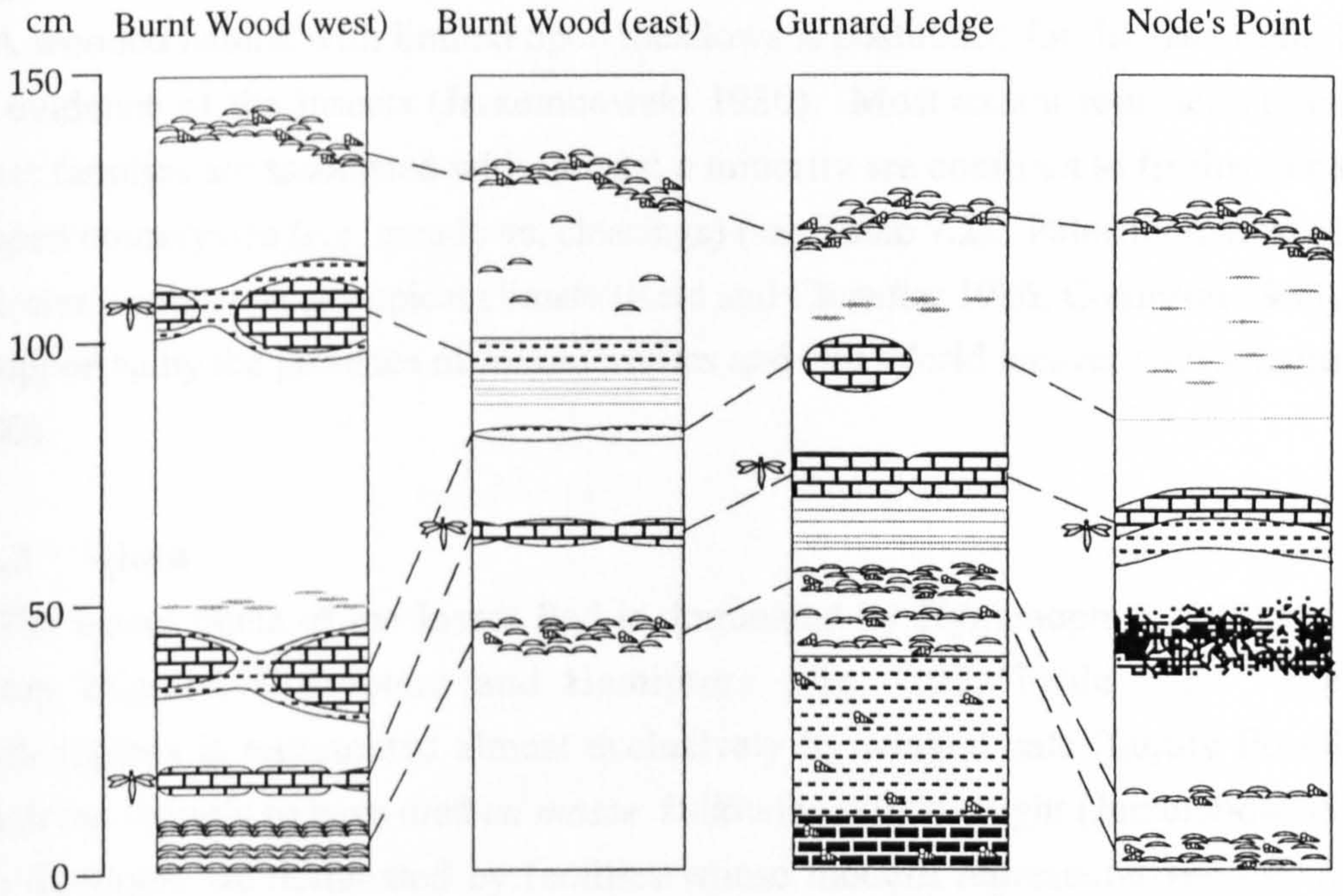


Figure 7.05 Stratigraphic position of the Bembridge Marls Insect Bed.



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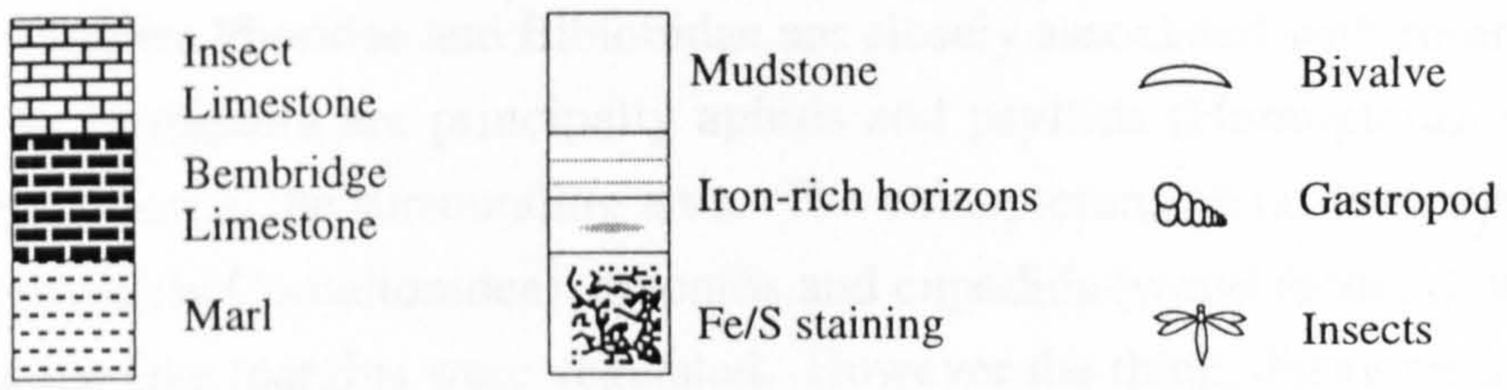


Figure 7.06 Logs of sections of the Oligocene Bembridge Marls Insect Bed, Isle of Wight, UK. (See Appendix A2.2 for detailed logs).

water rather than marine setting, since extant anostracans are known to inhabit small, temporary, alkaline water pools (Potts and Durning 1980). The presence of salt psuedomorphs indicate at least occasional supersaturation of the waters, while the absence of fish (save a single fish vertebrae: Reid and Chandler 1926) would seem to suggest that the waters were generally inhospitable.

A wooded habitat with limited open meadows is postulated for the lake hinterland on the evidence of the insects (Jarzembowski 1980). Most extant representatives of the insect families are associated with forests; a minority are confined to freshwater settings or open countryside (*e.g.* meadows, clearings) (see Table 7.2). Palaeobotanical evidence indicates a sub-tropical/tropical climate (Reid and Chandler 1926; Collinson 1983), which is supported by the presence of fossil termites and Old World weaver ants(Jarzembowski 1980).

7.3.3 Biota

The insect fauna of the Insect Bed is dominated by Hymenoptera, followed by the orders Diptera, Coleoptera and Hemiptera (Fig. 7.07, Table 7.2). The order Hymenoptera is represented almost exclusively by winged ants (family Formicidae), which are thought to have died *en masse* following nuptial flight (Jarzembowski 1980). The dipterans are dominated by families whose modern representatives live in moist habitats: Mycetophilidae (fungus gnats), Psychodidae (owl midges), Sciaridae (dark-winged fungus gnats), Sratiomyidae (soldier flies) and Tipulidae (crane flies) (Fig. 7.07; Table 7.2). Families Phoridae and Bibionidae are closely associated with rotting organic material. The Hemiptera are principally aphids and psyllids (Homoptera), indicating emergent vegetation in the surrounding area. The coleopterans so far identified include weevils (superfamily Curculionidea), apionids and cupedids (wood feeders), which also suggests that the lake margins were vegetated. However the thick, decay resistant elytra of coleopterans are not overrepresented. Indeed sixteen insect orders are known from the various collections, including the comparatively rare Psocoptera (barklice), and Isoptera (termites), and the fragile Thysanoptera (thrips), suggesting that the insect fauna is relatively representative of the original diversity (Table 7.2). No aquatic larvae have been reported. The lack of aquatic specimens may indicate that the waters were inhospitable.

McCobb *et al.* (1997, in review) employed cluster analysis to test the palaeoenvironmental reconstruction based on the insect taxa and to assess the sampling bias inherent in the Bembridge insect biota. The data and methods used were based on those employed by Henwood (1993) in an analysis of the insect fauna preserved in Eocene amber from the Dominican Republic. The comparison was based on twenty-seven modern, tropical insect faunas identified to ordinal level, as well as Dominican amber. The sampling bias was considered by comparing the Bembridge fauna with samples captured using different modern trapping techniques.

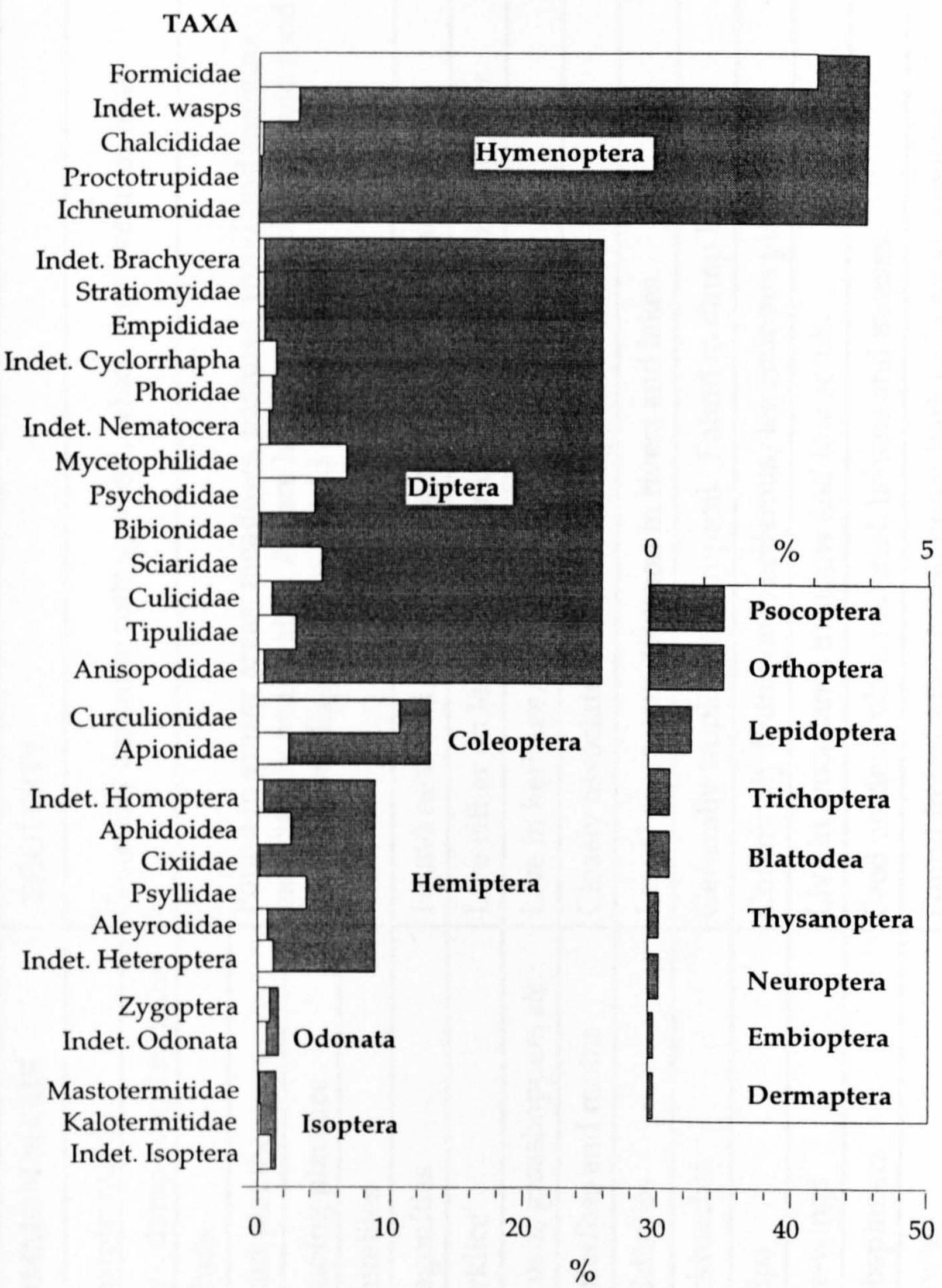


Figure 7.07 Relative proportions of the Bembridge Marls insect fauna.

ORDER	FAMILY	COMMON NAME	ECOLOGY
Isoptera	Mastotermitidae	mastotermitids	Generally consume rotting wood, which they live in or near.
	Kalotermitidae	dry-, damp-wood termites	
Homoptera	Aphidoidea	aphids	Found in grassy areas, meadows, pastures, woodland margins particularly near water. All are herbivorous, sucking liquid food from plants. Eggs tend to be laid inside plants.
	Cixiidae	cixiid planthoppers	
	Psyllidae	jumping plantlice	
	Aleyrodidae	whiteflies	
Odonata		dragonflies	Found near still/slow flowing water. Nymphs aquatic.
Psocoptera		barklice	Live either on leaves, twigs or under stones and in leaf litter.
Orthoptera		locusts, grasshoppers *etc.*	Live in herbage/leaf litter of woods and grassland.
Lepidoptera		butterflies and moths	Closely associated with flowering plants.
Trichoptera		caddisflies	Larval cases very common in rivers and lakes.
Blattodea		cockroaches	Generally tropical/subtropical. Found in damp leaf litter.
Thysanoptera		thrips	Commonly found on cruciferous/leguminous plants.
Neuroptera		lace-wings	Live in woodland, meadow and low scrub.
Embioptera		webspinners	Feed on dead plant material, lichens and mosses.
Dermaptera		earwigs	Found in leaf-litter, in soil under bark or in rocky crevices

ORDER	FAMILY	COMMON NAME	ECOLOGY
Hymenoptera	Formicidae	ants	Common in damp environments, often associated with flowering plants and fruit. Some are parasitic. Ants are entirely social, and are often found in large swarms. Tend to occupy the leaf litter, altho' marital swarms common.
	Chalcididae	chalcid wasps	
	Prototrupidae	proctotrupids	
	Ichneumonidae	ichneumonid wasps	
Diptera	Stratiomyidae	soldier flies	Dipterans occupy a range of environments. Some prefer moist wooded areas and meadows (Mycetophillidae, Stratiomyidae, Psychodidae, Bibionidae) often close to standing water such as lakes or streams (Tipulidae, Culicidae, Empidae). Phorids prefer rank vegetation and rotting organic material. The culicids have a close association with mammals.
	Empididae	dance flies	
	Phoridae	humpbacked flies	
	Mycetophilidae	fungus gnats	
	Psychodidae	owl midges	
	Bibionidae	March flies	
	Sciaridae	dark-winged fungus gnats	
	Culicidae	mosquitoes	
	Tipulidae	crane flies	
	Anisopodidae	window-midge	
Coleoptera	Curculionidae	weevils	Curculionids are associated with all vegetation.
	Apionidae	weevils	

The Bembridge insect fauna (together with that of Dominican amber) forms a distinct cluster with the Manaus and Osa primary tropical forests. The Osa sample was obtained using sweeps over the understorey vegetation of a primary forest in Costa Rica, 50-200m from the edge of a river. The vegetation consisted of adult shrubs and saplings of larger trees with a dense canopy above. The forest was occasionally flooded (Janzen 1973). The Manaus insects were collected using emergence and pitfall traps in primary terra firma forest in the central part of the Amazon Basin, which is subject to seasonal flooding (Penny and Arias 1982).

The common characteristics of these modern habitats define the likely palaeoenvironment of the Bembridge Marls. A primary sub-tropical forest, subject to episodic flooding or seasonal torrential rainfall, is probable, which is in broad agreement with the deductions of Jarzembowski (1980) based on the insect fauna.

Examination of sampling bias revealed that the Bembridge fauna clusters most closely with the Dominican Republic amber inclusions, and forms a distinct group with insects collected in tropical forests using emergence and pitfall traps. Both these types of trap sample insects from the leaf litter and lower herbage layers implying that the insect biota from the Bembridge Marls is biased towards organisms from these niches. Techniques which sample insects from high in the forest canopy (sweeps and fogging), the air (light and flight traps), and the soil, cluster much more distantly suggesting that insects from these niches are under-represented in the Bembridge Marls.

The remainder of the biota of the Insect Bed is composed of well preserved molluscs, crustaceans (anostracans, ostracodes, rare isopods), arachnids and birds (represented by feathers) (Woodward 1878, 1879; McCook 1888; Jones and Sherborn 1889; Jarzembowski, 1980). Fish (vertebrae) and fragmentary plant material including reeds and seeds, are reported (Reid and Chandler 1926; Collinson 1983).

7.3.4 Taphonomy

7.3.4.1 Introduction. The insect fossils of the Bembridge Marls are dominated by wings and elytra. Entire, three-dimensional specimens, preserving organics, are rare (Plate 7.9A). A spectrum of preservation exists, from complete and three-dimensional specimens with attached limbs to isolated fragments. Some specimens are preserved as voids lined with organic cuticle, but many exhibit some degree of internal mineralization.

7.3.4.2 Material and methods. Representative specimens (n=40, including two arachnids) from the Mitchell collection, Maidstone Museum and Art Gallery (England) specimens were examined using various techniques. Specimens which displayed features of interest under the light microscope (n=15) were examined under the SEM (Appendix A1.1). Specimens which revealed mineralized tissue (n=5) were analysed using the

electron microprobe (Appendix A1.2). Organic material from two specimens was examined using pyrolysis-gas chromatography/mass spectrometry (Appendix A1.4).

7.3.4.3 Cuticle.

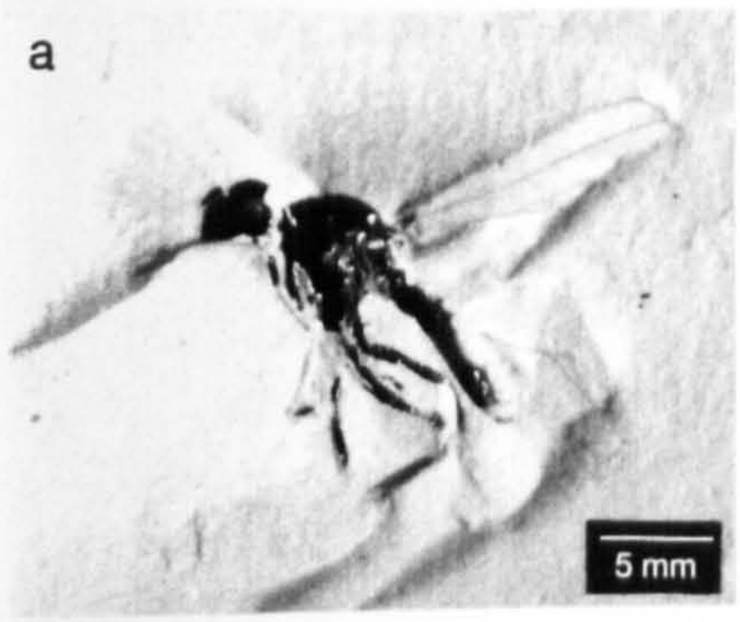
Morphology. The three-dimensional insects of the Bembridge Marls commonly preserve the cuticle as a thin layer of organic material. Insect cuticle consists of an outer epicuticle (3µm to 0.1µm thick), which lacks chitin, and an inner procuticle (10µm to 0.5mm thick) which consists of a thicker endocuticle overlain by a thinner sclerotized exocuticle (Neville 1975) and is composed primarily of chitin complexed with protein and a small amount of lipids (see Chapter 1, section 1.4).

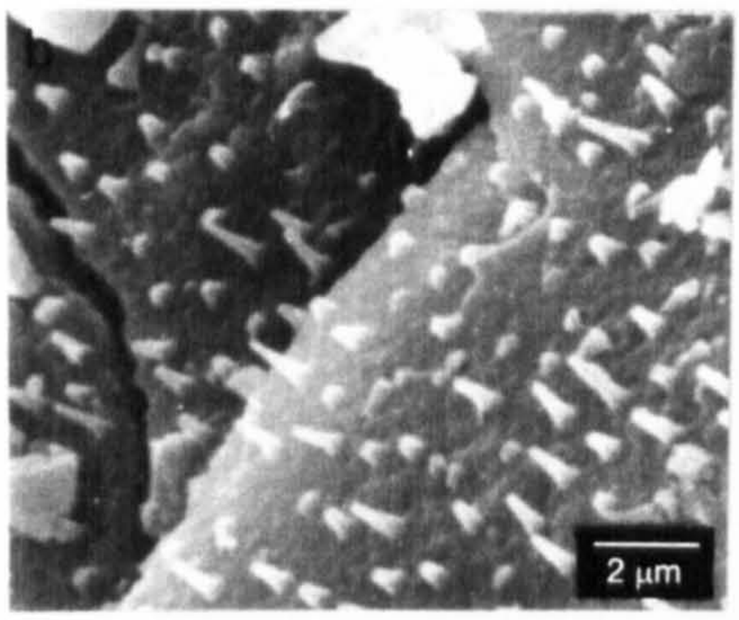
Scanning electron microscopy revealed that the external ornamentation of the cuticle of the Bembridge insects is preserved on a micron scale, including spines and pores (Plate 7.9B). Internally the parallel microfibrils that make up the procuticle appear to have been 'teased apart'. This may reflect more rapid degradation of the proteinaceous matrix than of the chitin microfibrils it binds (see also Chapter 8, section 8.6.3.3). Experimental decay of cuticles produces a similar appearance (see Chapter 2, section 2.7; Stankiewicz *et al.* 1997d). Scanning electron microscopy of the rare arachnids revealed pores on the surface of the cuticle (Plate 7.9D). Internally the cuticle consists of loose strands of organic material, which represent microfibrils that have separated following partial degradation (Plate 7.9E).

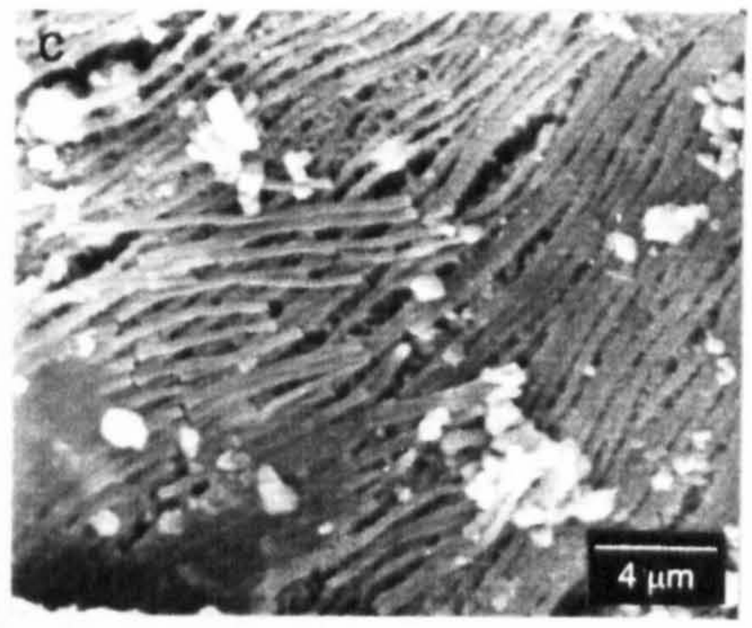
Composition. It is difficult to remove sufficiently large samples of cuticle from the specimens to allow analysis. Cuticle of two specimens was mechanically isolated from the sediment matrix. Neither yielded a chitin signature, even though traces of chitin have been obtained from insects of similar age elsewhere (Stankiewicz *et al.* 1997c). The organic material is aliphatic in composition, consisting of paired n-alk-1-enes and n-alkanes (Fig. 7.08).

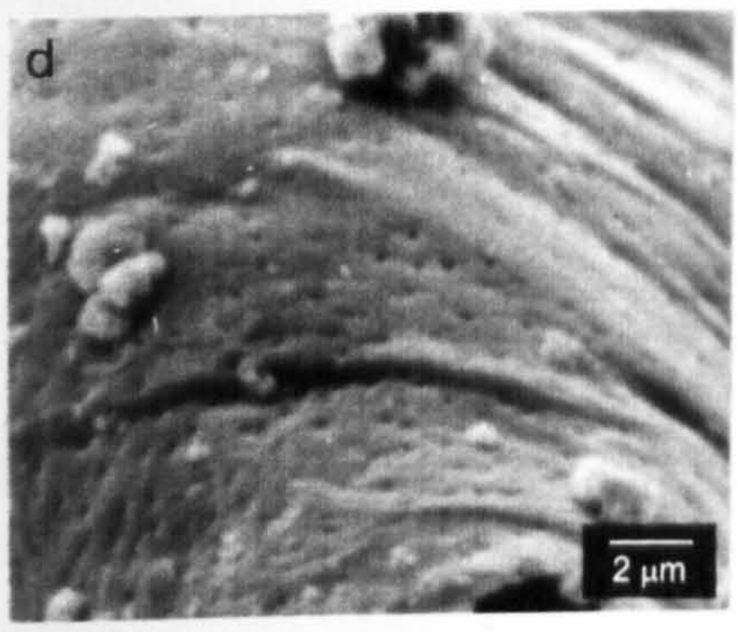
7.3.4.4 Internal tissue. Mineralized soft-tissue has been reported previously from the insects of the Bembridge Marls. Jarzembowski (1980) observed 'cream-coloured calcified muscle' in the abdominal area of an indeterminate papilionid (Lepidoptera) and used scanning electron microscopy to describe ultrastructural features of the wing scales of a hepialid (Lepidoptera). However, scanning electron microscopy of mineralized specimens for this project revealed only crude preservation of internal tissue. Lineations of sarcolemma and muscle fibres were evident in only two of the fifteen three-dimensional specimens examined (Plate 7.9F-H). Microprobe analysis revealed that calcite is the replacement mineral. The mineral infill in most specimens is a coarse crystalline fabric, with laths up to 50µm in length, which does not preserve the soft tissues.

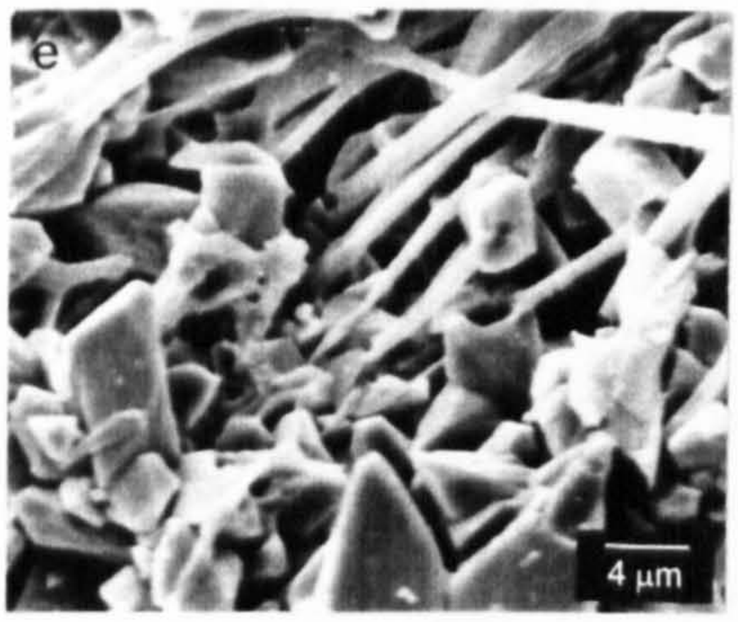
Plate 7.9 Arthropods from the late Eocene "Insect Bed", Bembridge Marls, Isle of Wight, UK. A, Three-dimensional dipteran preserving organic cuticle and mineralized internal tissues (BLS 504 A). *ca* x1.7. B-I Scanning electron micrographs. B, External view of insect cuticle (BLS 777). C, Microfibrils in insect procuticle (BLS 777). D, External view of arachnid cuticle (BLS 634). E, Microfibrils of arachnid procuticle with some calcite crystals (BLS 635). F, Calcified muscle fibres in insect (BLS 1130 A). G & H, Calcified sarcolemma in insect (BLS). I, Calcite crystals within an insect (BLS 633 B). All specimens from the Mitchell Collection, Maidstone Museum and Art Gallery.


a
5 mm


b
2 µm


c
4 µm


d
2 µm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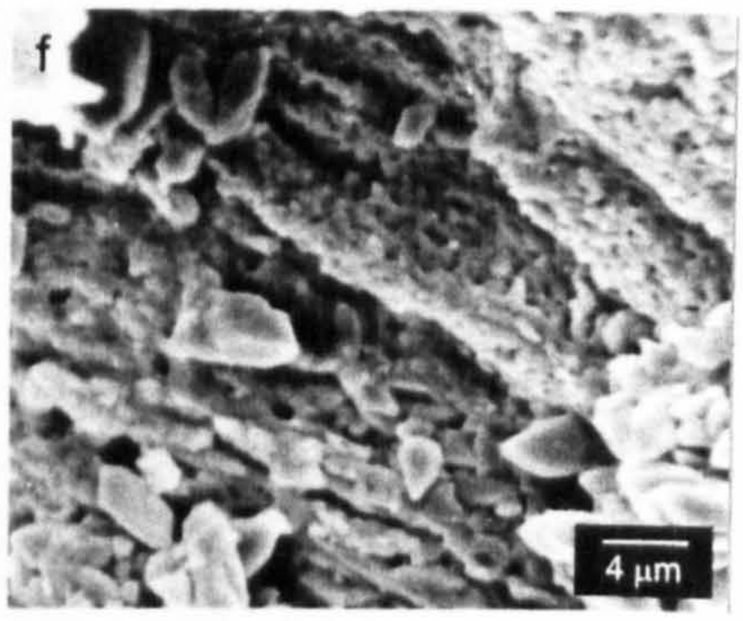
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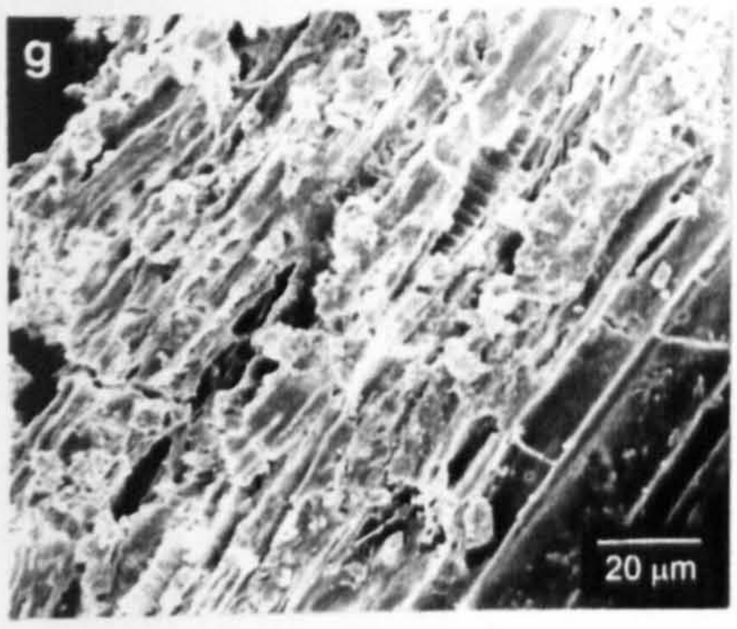
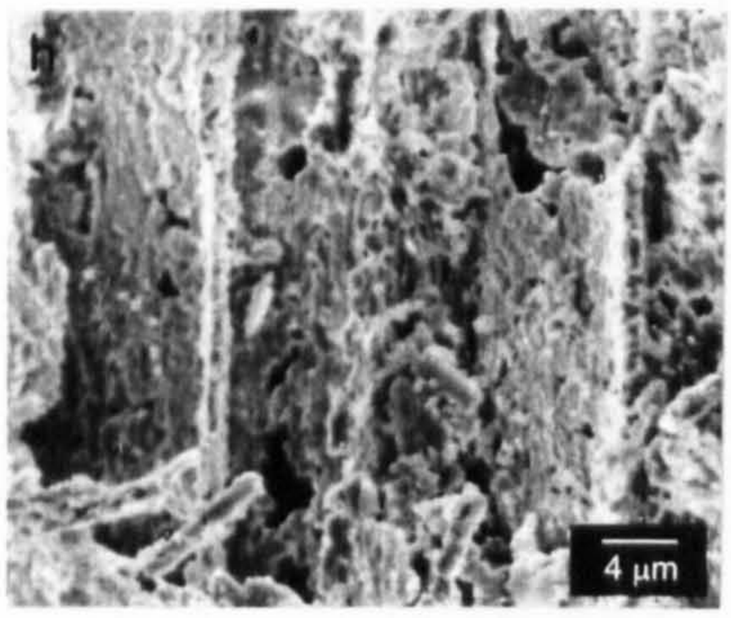

g
20 µm


h
4 µm

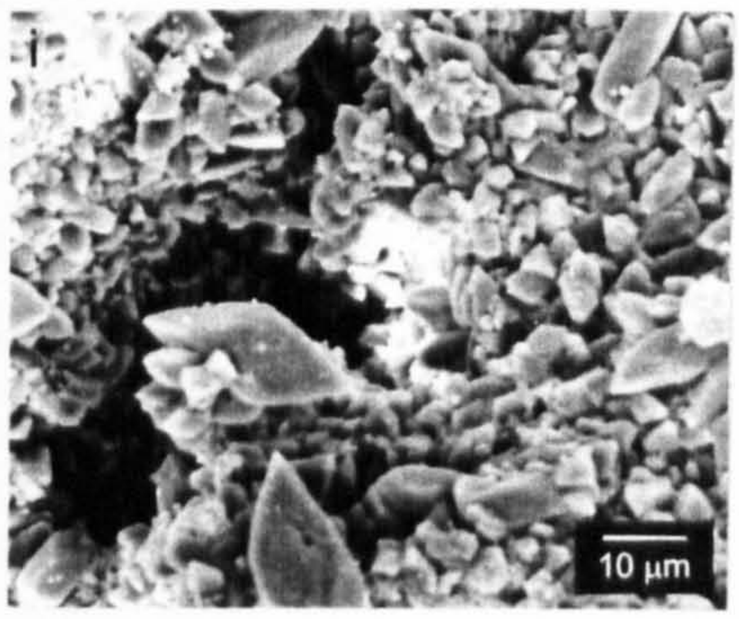
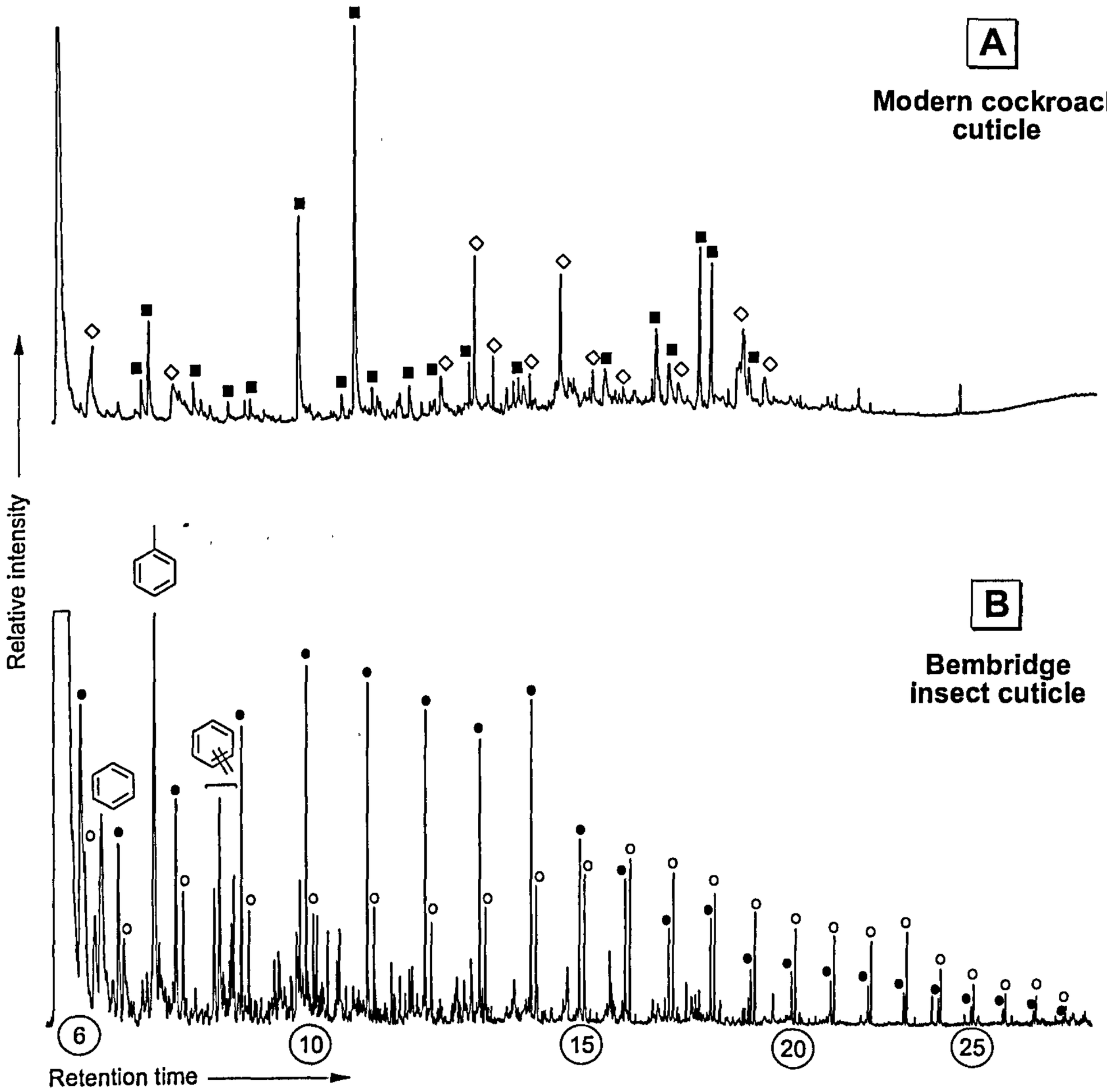

i
10 µm

Figure 7.08 Total ion chromatogram (pyrolysis at 610°C for 10 seconds) of (a) modern cockroach, and (b) insect cuticle from the Late Eocene Bembridge Marls. Diamonds are chitin markers, squares are proteins, black dots are alk-1-enes, white dots are alkanes.


A
Modern cockroach cuticle
B
Bembridge insect cuticle
Relative intensity
6
10
15
20
25
Retention time

7.3.5 Discussion

The occurrence of insects in full relief that retain organically preserved cuticle has earned the Insect Bed of the Bembridge Marls the label 'opaque amber' (Jarzembowski 1980). Specimens consist of moulds occasionally lined with organic material. The chitinaceous procuticle is retained, with surface ornamentation preserved, but the chitin-less epicuticle is not. The microfibrils of the endocuticle are 'teased apart'. Calcified tissue in the Bembridge fossils is rare. Although mineralizaed muscle is reported, the coarse crystalline nature of the calcite generally destroys all detail.

The experiments of Chapter 2 suggest that cuticle, comparable to that of the Bembridge specimens, occurs only in specimens which have decayed for some (~12 weeks in field based experiments). The 'teased apart' nature of the microbrils within the procuticle is the result of the decay of the interstitial protein matrix (Chapter 2; Chapter 8; see also Stankiewicz *et al.* 1997e, in review). Such degradation of the cuticle occurs only after much of the internal soft-tissue has deteriorated to an amorphous 'sludge', leaving only small isolated muscle fragments. The rarity of recognizable mineralized tissue in the Bembridge specimens may stem from the relative rarity of intact tissue in the decaying carcass. It is possible, however, that the soft tissues that are preserved were originally mineralized in apatite and only subsequently replaced by calcite, with a concommitant loss of detail (see Briggs and Wilby 1996).

The organic material of the cuticle of the Bembridge insects is aliphatic in composition, consisting of paired n-alk-1-enes and n-alkanes (Fig. 7.08). It was long assumed that the frequent occurrence of arthropod cuticles in the sedimentary record is the result of exceptional preservation of chitin, even in fossils as far back as the Cambrian (Carlisle 1964). However, recent analyses of arthropod cuticles ranging in age from the Silurian to the Cretaceous (Baas *et al.*1995; Stankiewicz *et al.* 1997a) have demonstrated that they are profoundly altered and that chitin is not preserved. So far chitin has been detected in only a very small number of examples of Tertiary and younger age (Stankiewicz *et al.* 1997b, c). A number of explanations have been advanced to explain the transfomation of fossil cuticle, including contamination by plant biomolecules (Baas *et al.*1995). Recent research suggests that this transformation may be the product of polymerization of lipids in the epicuticle or internal tissues during diagenesis (Stankiewicz *et al.* 1997a, 1997d, in review). The absence of chitin in the Bembridge Marls specimens shows that even where the morphology of the cuticle is well preserved, the chemistry may be dramatically altered.

The three-dimensional preservation must be the result of very early diagenesis of the calcareous matrix, which prevented the normal decay-induced collapse of the specimens. This process may be microbially mediated and occur more rapidly at the specimen/matrix interface as a result of decay within the carcass.

CHAPTER 8

RANCHO LA BREA

Stankiewicz, B.A. Briggs, D.E.G., Evershed, R.P. and Duncan, I.J. (1997) Chemical preservation of insect cuticles from the Pleistocene asphalt deposits of California, USA. *Geochimica Cosmochimica Acta* **8**, 2247-2252.

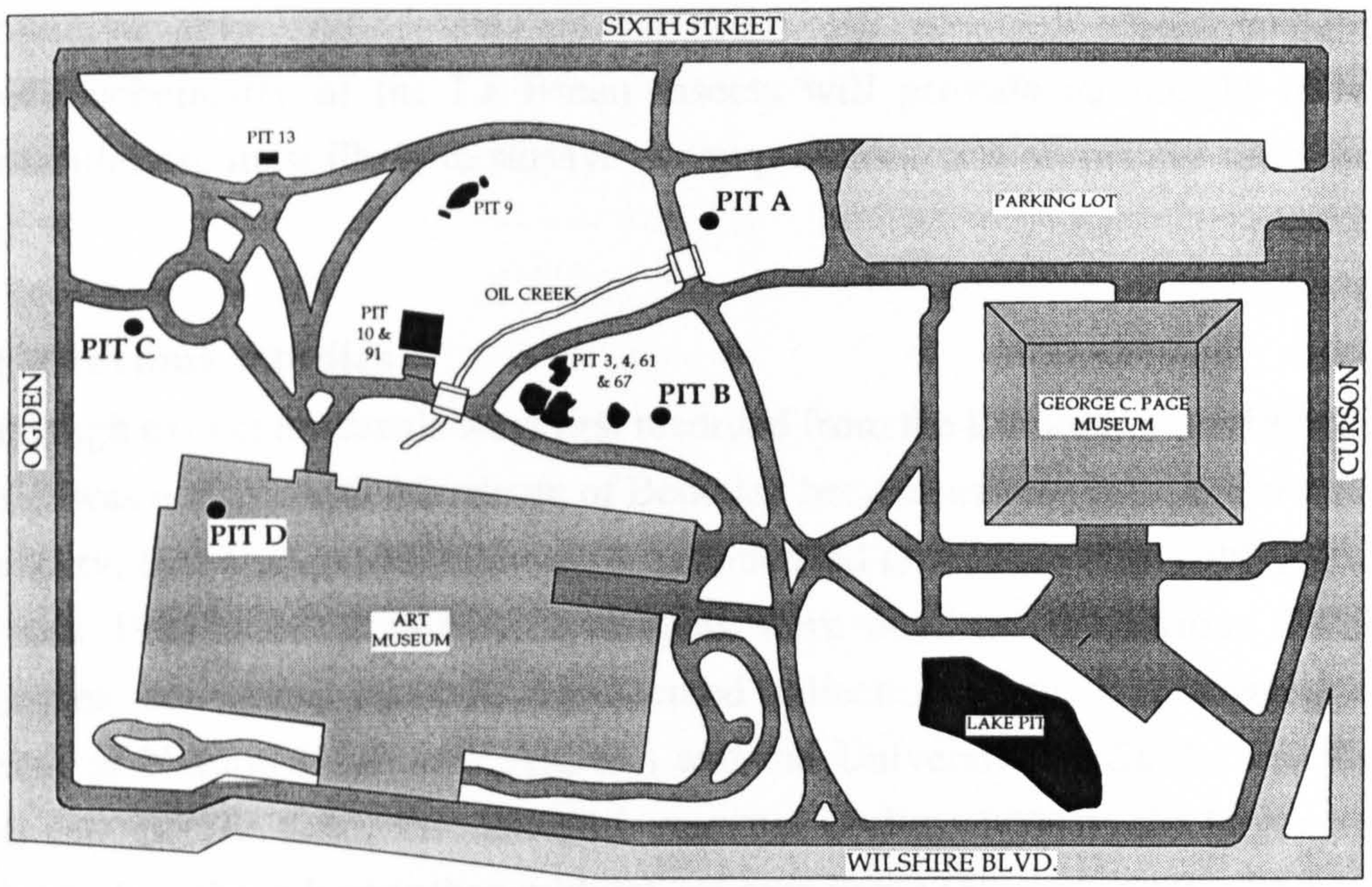
8.1 INTRODUCTION

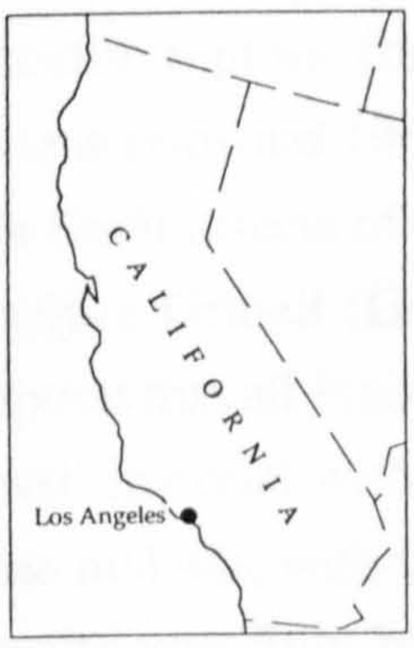
The Quaternary insect biotas are essentially modern. Non-mineralized specimens are common in peat bogs and fens, water-lain sediments and permafrost. Significant numbers are also recovered from asphalt, or 'tar', deposits. Mineralized specimens have been reported from a limited number of deposits (Girling 1979; Elias 1994). The value of Quaternary insects to palaeoecology, palaeoclimatic studies, insect zoography, even archaeology is now firmly established (Elias 1994). However, little work has been conducted upon their biochemistry or the nature of their preservation. This chapter will begin to address this deficiency by examining insects preserved in asphalt. Although insect-bearing asphalt deposits occur at a number of localities around the world: Talara, Peru (Churcher 1966), Fyzabad, Trinidad (Blair 1927), Binagady, Caucasus region of Russia (Bogachev 1948), the most famous and best documented is the Rancho La Brea Tar Pit of California (Fig. 8.01).

The Rancho La Brea site is now located in downtown Los Angeles, with the bulk of material recovered from 23 acres known as Hancock Park (Fig. 8.01), a National Natural Landmark since 1963 (Akersten *et al.* 1983; Stock 1992). The site is renowned for its vertebrates, among them 2,100 specimens of sabre-toothed cat (Miller 1968; Tejades-Flores & Shaw 1984). To date, some 600 animal taxa have been identified, 135 of them arthropod (Stock 1992). Over 100,000 individual arthropod specimens have been recovered, ~95% insects, with arachnids, ostracods, isopods, diplopods and chilopods completing the collection (Akersten *et al.* 1983). The fossils provide the basis for a near comprehensive reconstruction of life in the Los Angeles region of Southern California between 4,000 and 38,000 years ago (Stock 1992).

8.1.1 Aims and scope of work

Despite the fact that organic remains of arthropod cuticle are common in the fossil record, sometimes preserving remarkable morphology, the biochemistry is generally heavily altered (see Chapters 6 and 7.3; Baas *et al.* 1995; van Bergen *et al.* 1995; Stankiewicz *et al.* 1997a).





- Bliss (1929) Pit, no longer active
- Pit, active

Figure 8.1 Map of Hancock Park. No trace of the Bliss excavations of 1929 remain. (After Stock 1992, and Bliss 1929).

Such findings prompted the conclusion that the chitin biomolecule probably occurs only in unusual fossilization conditions such as oil seeps (Schimmelmann *et al.* 1988). The Rancho La Brea site of California is an asphalt deposit renowned for its fossil vertebrate, but from which insects are also commonly recovered. An understanding of the biogeochemistry of the La Brean insects will provide an insight into which biomolecules are most likely to survive decay processes and ultimately enter the fossil record.

8.1.2 Previous studies

Although extinct mammals were first recorded from the La Brea site in 1877 (Denton 1877), it was not until J.C. Merriman of Berkeley became aware of the site at the turn of the century, that serious scientific work commenced (Akersten *et al.* 1983). Between 1906 and 1915 about 2 million specimens were obtained by various Californian institutions, the largest and best documented collection by the Los Angeles County Museum of Natural History (L.A.C.M.) and the University of California, Berkeley (Stock 1992). The fossil assemblage is unusual in that ~90% of the larger mammal specimens (*i.e.* those bigger than rabbits) are carnivores (Marcus 1960). The avifauna are mostly raptors (orders Falcinoformes and Strigiformes), and exceed 90,000 specimens (Howard 1962).

The fossil insects of the Rosemary site tar pit, near Los Angeles, were first examined by Fordyce Grinell (Grinell 1908). He was one of the first workers to abandon the assumption that all Pleistocene fossils must represent extinct forms, and made matches of the fossil material with many modern species (Ashworth 1979). However, it was not until the mid 40s, with the work of W. Dwight Pierce, that the entomological significance of the site was fully revealed. Pierce began publishing on the Rancho La Brea and McKittrick sites in 1944, and continued for two decades (1946, 1948, 1949, 1954a, b, 1957). He was among the first workers to appreciate the significance of Quaternary insects as palaeoecological indicators (Pierce 1961; Ashworth 1979). However, his work was replete with error (Miller 1982). Serious problems resulted from his erection of taxa based on fragmentary specimens. Pierce felt that fragments that he could not assign to known taxa should be described as new taxa, so that they could be considered 'identified'. Most of his fossil material has been re-examined recently, and nearly all of the specimens have been matched with extant species (*e.g.* Miller *et al.* 1981).

8.2 GEOLOGICAL SETTING

The asphaltic beds are part of a Late Pleistocene alluvial sequence consisting of near horizontal beds of sand, clay, gravel and angular cobbles, 12 to 58m thick (Stock 1992). The underlying formations (Late Tertiary - Early Pleistocene) are folded and were deeply eroded prior to alluvial deposition (Eaton 1928).

Grant and Sheppard (1939) consider this alluvial sequence a marginal fan deposit (a number of which slope from the southern border of the Santa Monica Mountains). The La Brea fossils were thus preserved in gravels and sands accumulating on an outwash plain between the mountains and the Pacific Ocean. The main bone accumulations are restricted to the upper 9m of sediment, and are underlain by a bed of marine sand (Marcus & Berger 1984). The asphalt originates in petroleum from the Salt Lake oil field deep below the surface, and the widespread distribution of asphalt seeps suggests extensive sub-surface fracturing (Arnold 1907). Clustering of the fossil sites along an axis traversing Hancock Park is further evidence (Stock 1992).

The oldest fossils date to 32,000 years BP, the youngest to less than 6,000 years BP (dates derived from samples of bone collagen: Marcus & Berger 1984). Therefore, the Rancho La Brea fossil accumulated during the glacial maxima and the interstadials of the last (Wisconsonian) glaciation of the Pleistocene Ice Age (Stock 1992).

8.3 ASPHALT AND ENTRAPMENT

Akersten *et al.* (1983) found no evidence to support the popular notion of deep or laterally extensive pools of asphalt. The larger fossils occur primarily in fluvial sands with clay balls, gravel lenses, fish remains and aquatic specimens. Few specimens show any evidence of high energy transportation. Present data indicate that asphalt seeped up through the permeable sands of dry stream channels during warm summer weather. The more volatile constituents of the asphalt escaped as it exuded, leaving a denser encrusted residue. This surface rapidly hardens around the edge of the seep and gradually extends to the centre. As temperatures rise the crust softens, creating an effective and efficient trap operating almost unceasingly and capable of catching all manner of birds, mammals and insects. The resulting very shallow puddles of asphalt would often be concealed by leaves and dust (Stock 1992). Pools of water atop the asphalt may have attracted the thirsty. A single incautious creature mired in the asphalt would lure carnivores, which in turn would fall victim to the viscous material, increasing the bait for others (Stock 1992). The carcasses soon decayed and the skeleton disarticulated; individual bones, became saturated with asphalt and settled into the mire. During the subsequent winter rainy season, streams deposited a thin layer of sand over the now cooled and solidified asphalt. The warm weather of early summer then dried the streams and reset the trap. Although complicated by major floods, changes in base level, and lateral channel movement, repetition of the annual cycle built up the surface of the land to form the typical conical bone masses found at Rancho La Brea (Woodward & Marcus 1973).

A major entrapment (*e.g.* a large herbivore, four wolves, a sabre-toothed cat and a coyote) need occur only every decade to account for the immense number of fossil mammals recovered (Stock 1992). Carnivores, not unexpectedly, dominate the recovered

mammals, followed by those most susceptible to entrapment, the young, aged and maimed.

However, the actual method of fossil attraction and subsequent entrapment has yet to be thoroughly and satisfactorily explained (Akersten 1991; Quinn 1991). Domestic animals, including cows, are known to have been immobilized by asphaltic outflows only a few centimetres in depth, hence deep seeps are not essential for entrapment (Stock 1992). The relative scarcity of articulated or associated skeletons also argues against the wholesale entombment of complete animals (at least on a regular basis) with successful scavengers disarticulating and dispersing the carcasses. Birds (including waterfowl), small mammals and insects continue to be mired in asphalt flows today (Pierce 1949; Stock 1992; C. McNassor *pers. comm.*).

Five possible methods of entrapment have been proposed for insects, each of which has been observed in modern asphalt seeps (Miller 1982; Horvath & Zeil 1996). The relative importance of each factor is unknown, with each presumably responsible for attracting particular insects.

1. Attraction to carrion mired in the asphalt (Stock 1992). This is particularly important for scavenging insects and those which lay their eggs in or on flesh, *e.g.* carrion beetles (*Silphidae*), blow flies (*Calliphoridae*) and flesh flies (*Sarcophagidae*).

2. Attraction to pools of water atop the oil. This group is important to insects which lay their eggs in water. A swarm of dragonflies mired in the present day asphalt seeps of McKittrick, California is figured by Pierce (1949).

3. Attraction to the oil seeping from the asphalt. Insects which detect water by means of horizontal polarization of light reflected from the surface of water are often attracted to oil which closely mimics the polarization and reflectivity of water. This phenomenon has been noted in the oil ponds of Kuwait created following the Gulf War (Horvath & Zeil 1996).

4. Attraction to the asphalt itself. Some insects are attracted to freshly tarred road surfaces (Saylor 1933; Borrell 1936; Hubbs & Walker 1947) while others are attracted to burning oil (Van Dyke 1926; Linsley 1933). Anecdotal explanations of such attraction suggest that the insects may be attracted to the warmth of the road, or the scents released by the hot or burning tar (Miller 1982).

5. Accidental trapping (without attraction). Insects crawl or fall into the asphalt and cannot free themselves.

While the larger and more continuous fossil accumulations represent extrusive entrapment, many of the smaller accumulations probably represent fluvatile concentrations of bones within reactivated stream channels (Miller 1982). Following deposition, the fossils were impregnated by the subsequent summer asphalt rise. Re-interpretation of stratigraphy and radiocarbon dating has allowed correlation of the

stratified asphalt deposits with the facies of surrounding sediments that are not oil impregnated.

Fluvial sedimentation also accounts for the introduction of secondary material, some of which may have been transported considerable distances (Akersten 1991); such fluviatile accumulations were secondarily impregnated by asphalt (Doyen & Miller 1980; Miller 1982, 1983; Scott 1989).

8.4 INSECT BIOTA

Much of the insect material is recovered from the matrix infilling the brain cavity of large vertebrate skulls (Miller 1979). The remains are usually fragmentary body parts and disarticulated heads and wings, although complete specimens are not uncommon. Many of the insects possess heavily sclerotized chitinous exoskeletons.

The La Brea insects can be placed in the following crude palaeoecological classification (Miller 1982):

1. Aquatic and semi-aquatic species which lived in water overlying the tar or were attracted to the tar, mistaking it for water:

2. Scavenging species living on or attracted to the carrion and dung:

3. Ground-dwelling beetles and other terrestrial crawling species living in proximity to the seeps:

4. Miscellaneous stray individuals of herbivorous or other species which are not preserved in significant numbers:

5. Fragments of insects from faeces and gut contents of vertebrates:

Representatives of the orders Orthoptera, Hemiptera, Homoptera, Coleoptera, Hymenoptera and Diptera have been reported (Miller 1979, 1982, 1983; Miller *et al.* 1981; Miller & Peck 1979; Moore & Miller 1978). Beetles dominate the fauna: representatives of twenty-five families have been recovered including water (*Dytiscidae* and *Hydrophilidae*), carrion (*Silphidae*), predaceous, dung (*Scarabaeidae*), ground-dwelling (*Carabidae*) and plant feeding (*Dascillidae* and *Chrysomellidae*) beetles. The darkling ground beetle (*Tenebrionidae*) is the most abundant.

Insects are important to the palaeoecological reconstruction of the region. The abundant darkling ground beetles suggest a semi-arid coastal scrub or dry woodland environment, similar to southern California today, where these beetles persist (Doyen & Miller 1980). Water beetles and water bugs indicate the presence of standing water. Several kinds of insects are recognized that today characterise particular stages in the sequence of decay. Blow flies (*Calliphoridae*) and fleshflies (*Sarcophagidae*) appear soon after death. Subsequent post-mortem stages are identified by the presence of dermestid, silphid (burying and carrion), and histerid beetles. Comparative study of decaying mammals today indicates that vertebrate carcasses must have been exposed in and about the traps for at least five months (Miller 1982). Some of the scarab beetles

recovered at La Brea, belong to a family whose closest living relatives inhabit mammalian dung (Miller 1982).

8.5 GENERAL TAPHONOMY

The fossils of Rancho La Brea represent both an extinct fauna, (usually the larger animals) and a living fauna (usually the smaller animals, insects and plants). Different elements present in the biota suggest different environmental conditions: mastodon, peccaries, deer and timber wolf indicate forest conditions; camel, bison, horse and other mammals, the prairie (Stock 1992). Interpretation of the age and geometry of the accumulations is hampered by the episodic nature of the asphalt seepage, with a single accumulation representing a number of temporal intervals. Also, new accumulations may form at topographically lower elevations than adjacent older ones due to the cut and fill nature of fluviatile deposition.

Articulated skeletons of large birds and mammals are known, but are uncommon; La Brea deposits rarely yield even two associated bones (Akersten *et al.* 1983), although it appears probable that the various elements of individual skeletons are found in close proximity (Stock 1992). Carcasses emergent from the asphalt would be dismembered by scavengers, and the pieces strewn around the margins of the seep, where they were devoured, damaged or destroyed. The remaining carcass would ultimately become submerged in the protective asphalt. Skeletal elements exhibiting the bite marks of scavengers provide further evidence of dismemberment prior to immersion, as do bones which exhibit weathering effects (Akersten 1980).

The peculiar nature of the embedding material - a heavy oil, soft or frequently granular asphalt, has largely been responsible for the excellent preservation. The microstructure of bones and teeth is well preserved (Doberenz & Wyckoff 1967), with up to 80% of the original collagen remaining (Ho 1965). The amino acid ratio of the collagen is comparable to that of related extant species (Ho 1967). Beside bones and teeth, soft tissue is also recorded including the cuticle of insects (Miller 1979, 1982) and the tracheal rings of birds (Shaw & Quinn 1986). However feathers, the horny bills or talons of birds, and the hair or strong claws of mammals are absent (Stock 1992). Wood is common. Leaves are noted, though often preserved only as impressions (Stock 1992).

8.6 FOSSIL PRESERVATION

8.6.1 Introduction

The decay of chitin in terrestrial environments is poorly understood (Stankiewicz *et al.* 1996). While it is widely accepted that the preservation potential of chitin is enhanced where it is cross-linked in robust sclerotized cuticle, little work has been done to establish this fact either experimentally or by examination of the recent fossil record. Laboratory

experiments conducted upon marine organisms have demonstrated that while chitin is relatively resistant to degradation, the protein component is more readily biodegraded (Baas *et al.* 1995). Although recognisable quantities of the chitin monomer have been demonstrated in Quaternary beetles (Miller *et al.* 1993), it is clear that chitin only survives in a recognisable form in fossils under exceptional circumstances.

Despite the fact that organic remains of arthropod cuticle are abundant in the fossil record, sometimes preserved with remarkable morphological detail (see Chapter 7), the original chemistry is generally altered to an aliphatic polymer characterised by a homologous series of alkanes and alkenes upon pyrolysis (Baas *et al.* 1995; van Bergen *et al.* 1995; Stankiewicz *et al.* 1997). The origin of these diagenetic products and the elucidation of the chemical pathways involved are currently under investigation (Baas *et al.* 1995; Stankiewicz *et al.* 1996, 1997a, b). Such results prompted the conclusion that the preservation of chitin derivatives such as amino sugars and amino acids probably occur only in unusual fossilization conditions such as oil seeps (Schimmelmann *et al.* 1988; see also Stankiewicz *et al.* 1997b).

Flash pyrolysis-gas chromatography/mass spectrometry (py-GC/MS) is particularly appropriate to the study of insoluble materials available only in minute quantities (*e.g.* Simmonds 1970; van Bergen *et al.* 1995), and has previously been used to analyse chitin (van der Kaaden *et al.* 1984; Franich *et al.* 1984; Davies *et al.* 1985; Baas *et al.* 1995) and proteins/amino acids (Tsuge & Matsubara 1985; Munson & Fetterlof 1987; Boon & de Leeuw 1987). Only recently, however, has py-GC/MS been applied successfully to detect these biopolymers in animal cuticles where chitin and proteins are cross-linked (Stankiewicz *et al.* 1996a). Consequently this technique was employed to investigate the state of preservation of chitin and protein biopolymers in insect remains from the Pleistocene Rancho La Brea deposit of California.

8.6.2 Materials and method

The fossils insects examined in this study were recovered by Wes Bliss during the 1929 field season at Hancock Park (C. McNassor, *pers comm.*). Four pits were excavated during that year (A, B, C, D) (Fig. 8.01). The larger pits B and C, were substantial (depths up to 27 feet) and produced only vertebrate material: sloth, camel, wolf, sabre tooth tiger, a single mastodon tusk and many avian bones. The remains were concentrated by alluvial activity, not mired by surface asphalt pools, and were associated with gravel and boulders which were later impregnated by rising asphalt (Bliss 1929). Little information is available on Pit D. It seems to have produced predominantly avian and rodent bones (Bliss 1929). The insects were recovered from Pit A, a shallow, 7ft diameter excavation where they are associated with fine material, primarily plant remains, and the bones of birds and rodents (Bliss 1929).

Specimens of Coleoptera and Orthoptera were obtained from the Bliss 1929 pit (~6,000 - 32,000 BP: Stock 1992). The asphalt was originally collected by trenching,

sieved and washed in kerosene. Immediately prior to analysis, the cuticle samples were further solvent extracted with CH_2Cl_2 in order to minimize the influence of contaminants such as asphalt. The samples (see Table 8.1) were then analysed using py-GC/MS (see Appendix A1.5), and examined under the SEM at a low kV (see Appendix A1.1).

Specimen	**Part analysed**
Coleoptera (La Brea, 13651)	Elytra
Coleoptera, Tenebrionidae (La Brea, 13647)*	Pronotum
Orthoptera (La Brea, 13642)*	Leg
Orthoptera, Acrididae (La Brea, 13641)	Leg

*represented on Plate 8.1.

Table 8.1 List of the samples analysed in the course of the study.

8.6.3 Results and discussion.

8.6.3.1 Preservation of chitin biopolymer. Pyrograms of four different cuticles of beetle and cricket specimens analysed from Rancho La Brea revealed a striking similarity in the relative abundance and distribution of pyrolysis products. Reconstructed ion chromatograms (R.I.C.) of specimens from Rancho La Brea (Fig. 8.02a-c) illustrate the pyrolysates characteristic of the material. All the prominent pyrolysis products of commercial chitin, including acetamide (4), pyridinecarboxaldehyde (7), acetylpyridone (9), 3-acetamidofuran (10), 3-methyl-5-acetamidofuran (11), 3-acetamido-2-pyrone (12) and 1,6-anhydro-2-acetamido-2-deoxyglucose (14), are present in the cuticle of the fossil specimens (see Stankiewicz *et al.* 1996). Pyrolysis products characterized by specific *m/z* 84 base peak (13-13"), which are interpreted as oxazoline-type structures (van der Kaaden *et al.* 1984), are major components of the fossil cuticles (Fig. 8.02a-c). Most of the chitin markers observed in the fossil samples can be identified easily in the complex RIC of fresh modern beetle cuticle (Fig. 8.02d). This is indisputable evidence for the exceptional state of preservation of the chitin polymer in the La Brea insect cuticle. Moreover, the presence of acetylated pyrolysis products (8-12) indicates that extensive deacetylation of the chitin to chitosan has not occurred.

8.6.3.2 Fate of proteins/amino acids. The pyrograms of modern beetle cuticle (Fig. 8.02d; see also Chapter 2) show an overwhelming dominance of the pyrolysis products of proteins rather than chitin, which reflects the average chitin (40%) and protein (60%) content found in Coleoptera and Orthoptera exoskeletons (Muzzarrelli 1977). The most prominent pyrolysis products are derived from amino acids such as tyrosine (F, G, H), tryptophan (I, J), phenylalanine (B, D), hydroxyproline and proline

Peak*	MS characteristics	Compound name	Origin
(1)	60	Acetic acid	Chitin
(2)	79, 52	Pyridine	Chitin
(3, A)	67, 55	Pyrrole	Ch, Pro
(4)	59	Acetamide	Chitin
(5)	93, 66	Methylpyridine	Chitin
(6)	109, 81, 53	Methylpyridone or Hydroxypyridine†	Chitin
(7)	107, 79, 51, 78	2-Pyridinecarboxaldehyde [T]	Chitin
(8)	127, 42, 85	Acetylpyrrolidone¶ [T]	Chitin
(9)	137, 109, 95, 81, 68, 53	Acetylpyridone¶†	Chitin
(10)	125, 83, 54, 42, 53	3-Acetamidofuran††	Chitin
(11)	139, 97, 69, 42, 53	3-Acetamido-5-methylfuran††	Chitin
(12)	153, 111, 82, 42, 83	3-Acetamido-4-pyrone††	Chitin
(13,13',13")	167, 84, 55, 83, 42	oxazoline structure†	Chitin
(14)	204, 59, 101, 114, 57	1,6-anhydro-2-acetamido-2-deoxyglucose†	Chitin
(B)	92, 91	Toluene	Phe
(C)	81, 80, 52, 50	C_1-pyrrole	Hpro
(D)	104, 78, 51, 103	Styrene	Phe
(E)	95, 94, 66	C_2-pyrrole	Hpro
(F)	94, 66	Phenol	Tyr
(G)	108, 107, 77, 79	3- and 4-methylphenol	Tyr
(H)	120, 91, 65	Vinylphenol	Tyr
(I)	117, 90, 89, 63	Indole	Trp
(J)	131, 130, 77	C_1-indole	Trp

*Numbers in parentheses refer to peaks on the chromatograms (Figure 8.02)

[T] Based exclusively on interpretation of mass spectra and NIH mass library

† Follow van der Kaaden *et al.* 1984; †† Follow Franich *et al.* 1984.

Table 8.2 List of major chitin and protein pyrolysis products recognised in the pyrolysates of Rancho La Brea fossil insect cuticles. Masses in bold indicate base peak and masses underlined indicate molecular weight (MW).

Figure 8.02 Reconstructed ion chromatograms (pyrolysis at 610°C for 10 sec) of (A) commercial chitin (Aldrich), (B) leg from orthopteran (13642) from Rancho La Brea, (C) pronotum from tenebrionid coleopteran (13647) from Rancho La Brea, (D) elytra from modern mealworm beetle (*Tenebrio molitor*). Numbers indicate major pyrolysis products derived from chitin and amino acids (details in Table 8.2), m - other important components directly related to chitin polymer, n - pyrolysis products of catechol moieties, t - pyrolysis products of proteins with 2,5-diketopiperazine structure, u - alkylated naphthalenes derived from pyrolysis of asphalt in which samples were preserved. Chemical structures are given for the most important pyrolysis products derived directly from chitin or amino acid moieties.

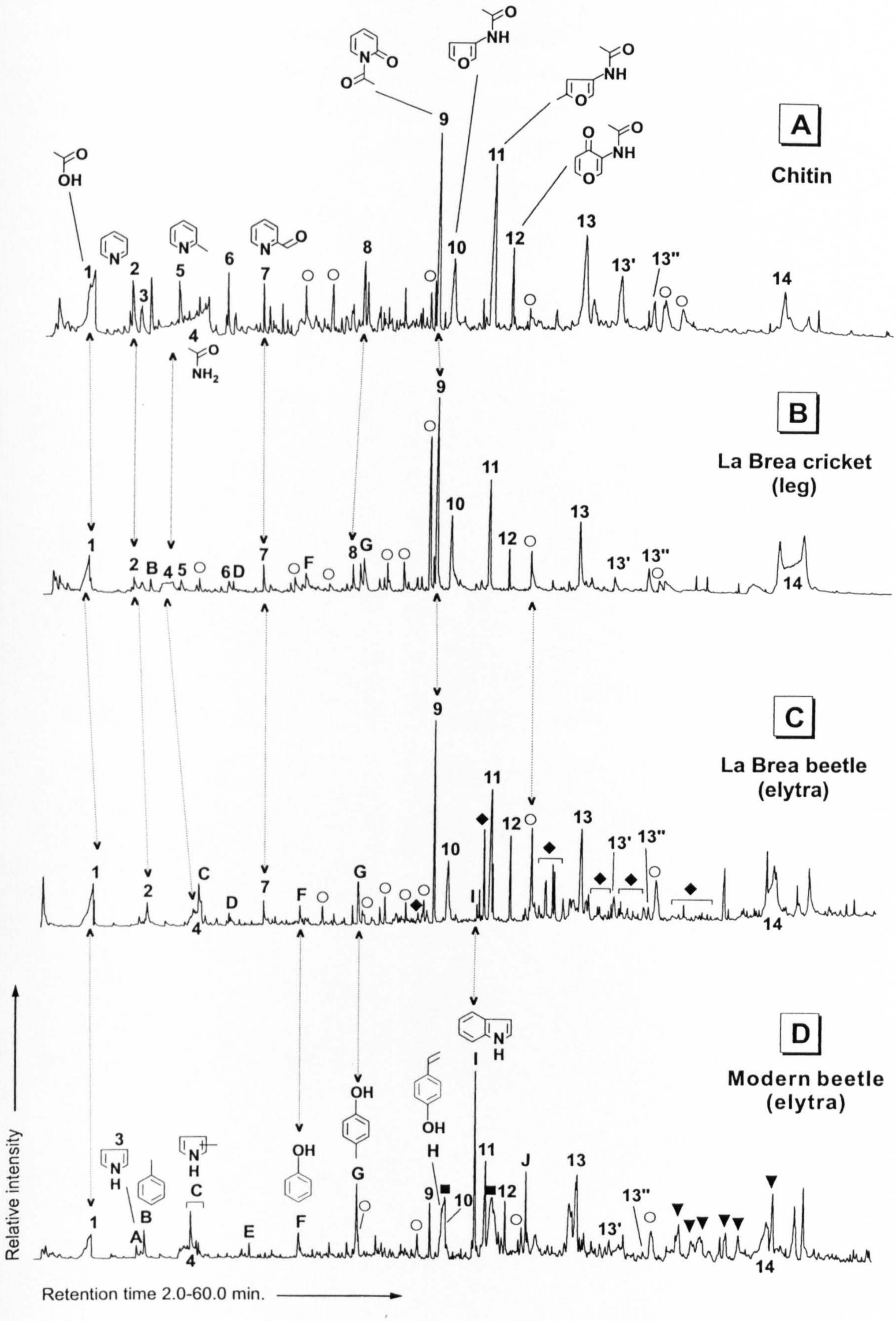
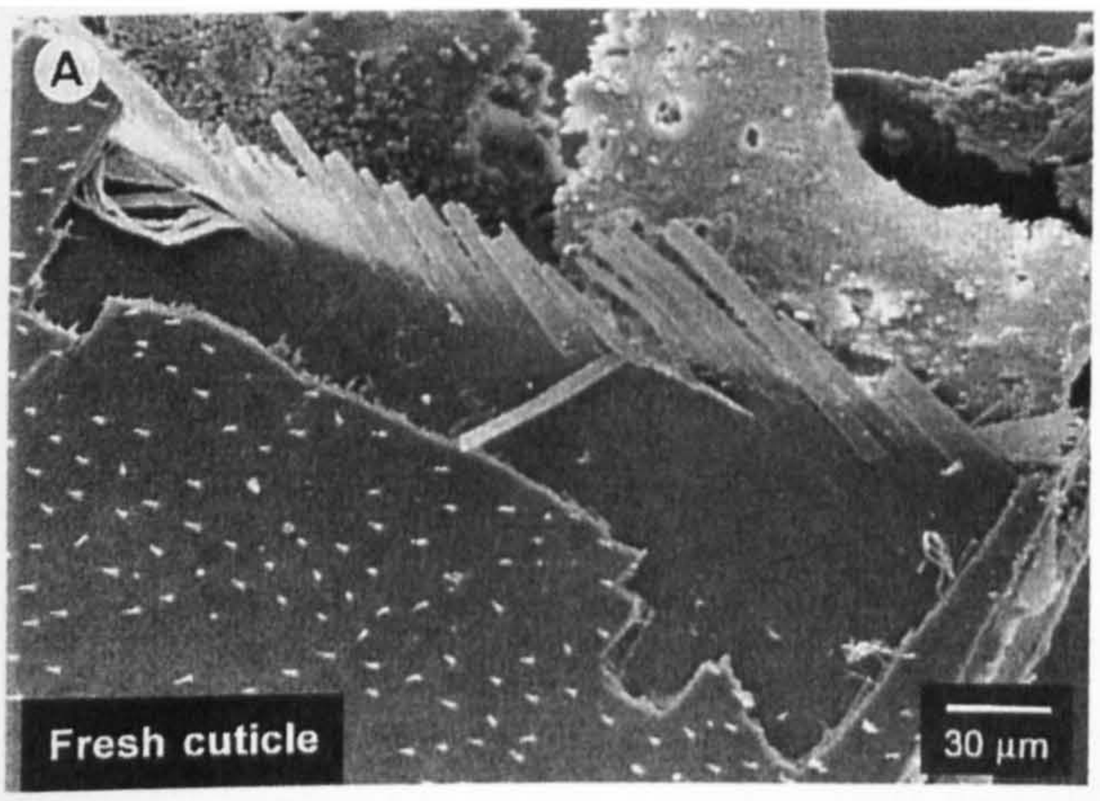
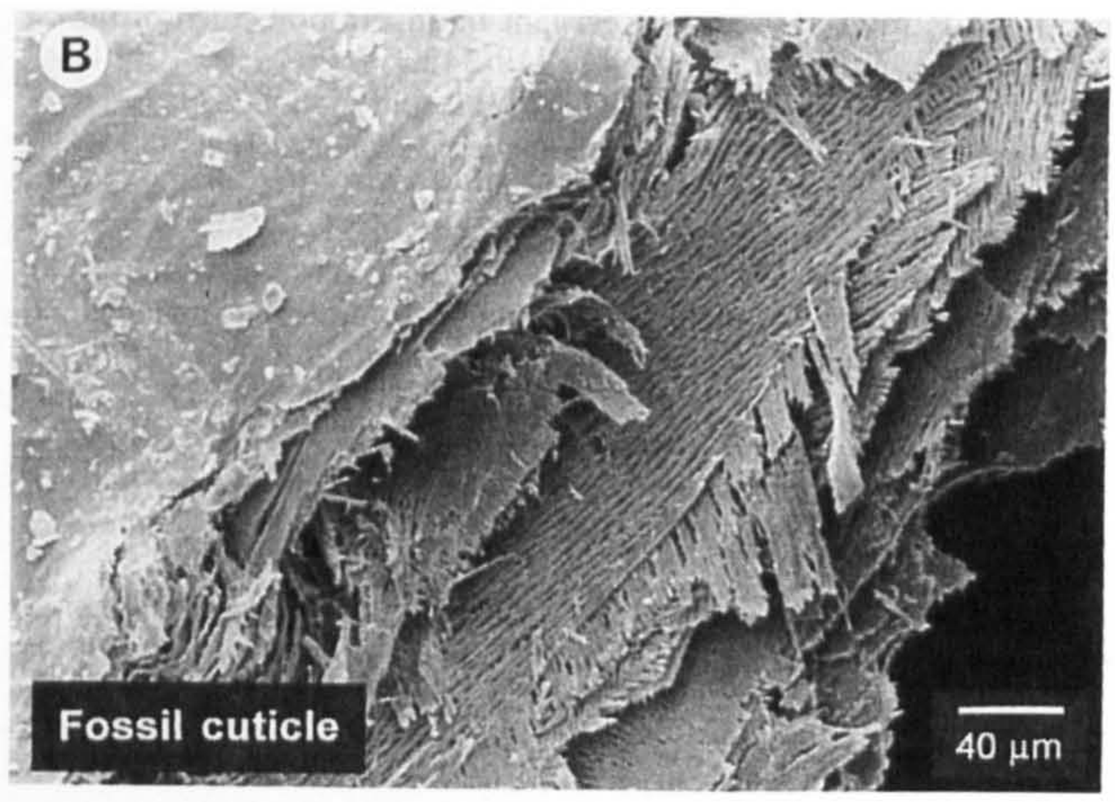
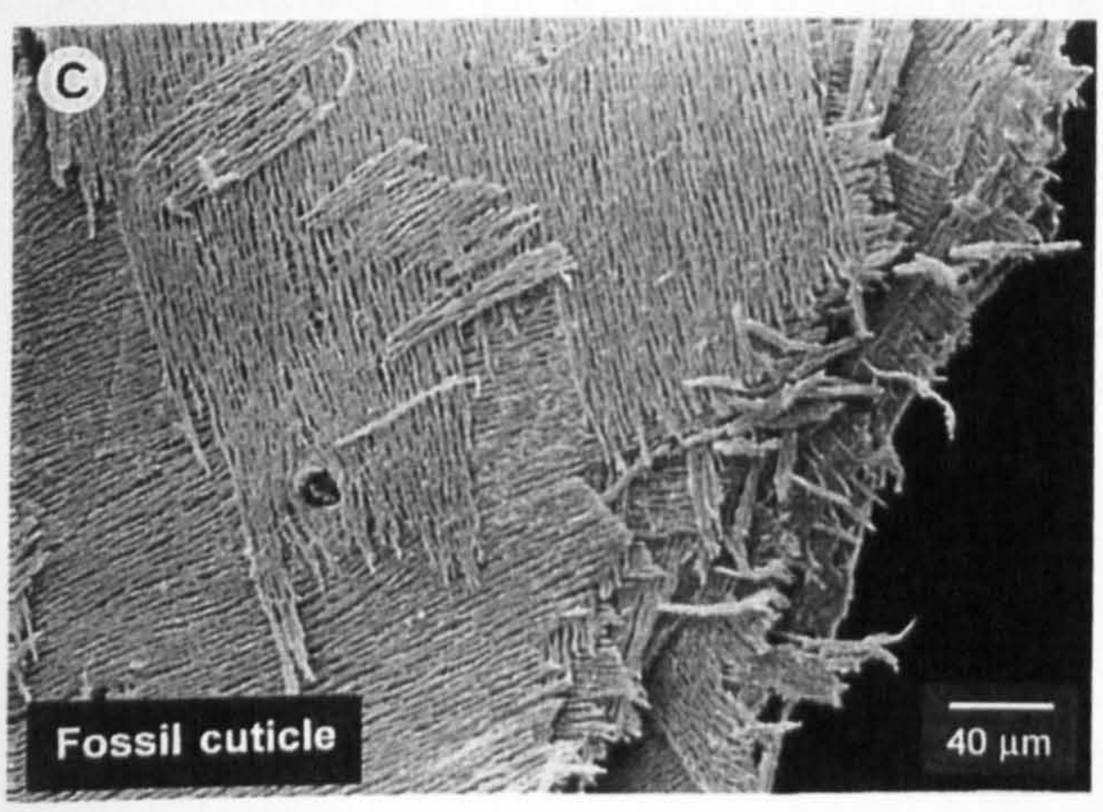
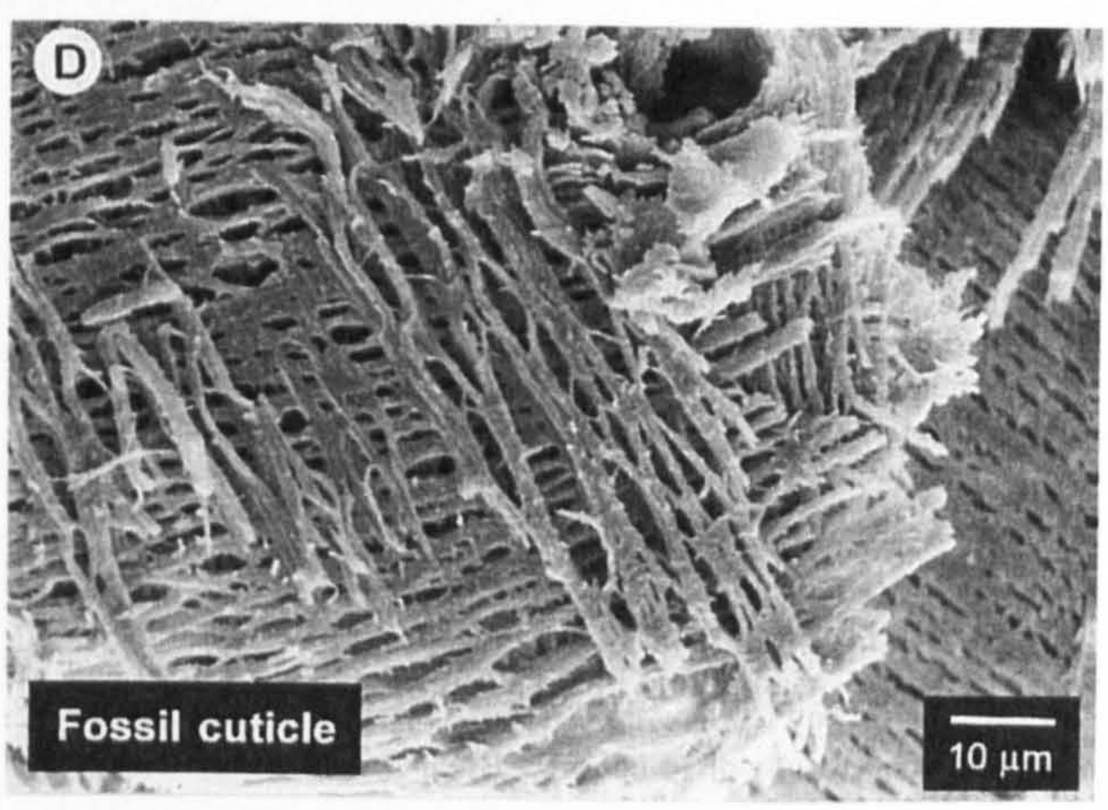

A
Chitin
B
La Brea cricket
(leg)
C
La Brea beetle
(elytra)
D
Modern beetle
(elytra)
Relative intensity
Retention time 2.0-60.0 min.

Plate 8.1 Scanning electron photomicrographs of fresh and asphalt beetles. A, fresh mealworm beetle cuticle showing overlapping layers of fibres enclosed by a matrix within the procuticle. The epicuticle is ornamented with fine spines. B-D, Rancho La Brea beetle cuticles showing overlapping layers of fibres (chitin) but without an intervening matrix (*cf* Chapter 2, Plate 2.1).


A
Fresh cuticle
30 µm


B
Fossil cuticle
40 µm


C
Fossil cuticle
40 µm


D
Fossil cuticle
10 µm

(A, C, E). Alanine, glycine and valine are also significant products of the cricket cuticle (Stankiewicz *et al.* 1996). Very specific protein markers such as 2,5-diketopiperazines which occur later in the RIC indicate that peptide moieties such as proline alanine (pro-ala), proline valine (pro-val), proline arginine (pro-arg) or proline-glycine (pro-gly) (Munson and Fetterolf, 1987; Stankiewicz *et al.* 1996) are also present. Comparison of the modern and fossil cuticles clearly reveals a greatly reduced protein content in the latter, implying some biodegradation before microbial activity was inhibited by the asphalt. The lack of catechols or histidine pyrolysis products, combined with evidence for severe degradation of proteins, suggests that the catecholamine and histidyl linkages are cleaved first, enabling further alteration of the protein moieties. However, phenols, indoles and cyanobenzenes, pyrolysis products of the 'non-chitin' constituent such as tyrosine, tryptophan and phenylalanine, are evident as minor components in the RICs of the fossil samples. These demonstrate at least partial survival of proteinaceous moieties, and imply that these particular amino acids are resistant to degradation. Although selective decay of proteins and preservation of chitin has been observed in laboratory decay experiments (Baas *et al.* 1995), this is the first demonstration of the phenomenon in fossil insects (see also Stankiewicz *et al.* 1997b).

8.6.3.3 Structural preservation. In hand specimen, the insects appear as hollow sacs of chitin, generally stained black. The appendages are disarticulated, although this is predominantly the result of methods of disinterment, since individual legs are frequently recovered (C. McNassor, *pers. comm.*). Beetles are the most commonly recovered invertebrate.

Scanning electron microscopy of fresh insect cuticle reveals overlapping layers of fibres which pull out of the enclosing matrix when the cuticle is fractured (Plate 8.1a). The decay experiments of Chapter 2 indicate that these predominantly chitinaceous fibres survive after the proteinaceous matrix decays. The insect cuticles of Rancho La Brea reveal overlapping layers of fibres without any intervening matrix (Plate 8.1b-d). Thus the predominant chitin composition of these fossil cuticles reflects the decay-induced in the destruction of the interstitial protein before further decay was inhibited by the asphalt. This is borne out by the lack of evidence of catechol moieties in the pyrolysates of the fossils even though these structures, which cross-link the chitin and protein constituents of cuticle (Schaefer *et al.* 1987), are abundant in the pyrolysates of modern beetle cuticle.

CHAPTER 9

SYNTHESIS

9.1 INTRODUCTION

Insects dominate the planet. They have colonised almost every possible ecological niche from the air above to the ground below, from the shore to the mountain summit. Such success is the result of a unique body plan which has a number of specialised features (see CHAPTER 1) but perhaps more importantly a flexibility of morphology which has allowed variation about a simple body form. It is this adaptation that has allowed insects to dominate such a range of environments. It is also the reason why insects are a particularly important environmental indicator, a fact which can be readily exploited in the examination fossil material.

Although the fossil record of soft-bodied organisms is traditionally considered inferior in quality to that of biomineralized taxa, recent studies have emphasised the importance of data provided by Konservat-Lagerstätten (see Allison and Briggs 1993). Insects are amongst the most commonly fossilised soft-bodied animals and their record is extensive (Labandeira and Sepkoski 1993; Jarzembowski and Ross 1993; Elias 1994). However, the conditions required for such exceptional preservation are by their very nature selective and responsible for considerable taphonomic bias.

This thesis represents the first taphonomic study of insects as a whole and of the biases that variation in their preservation imparts. While there have been some limited studies (*e.g.* Lutz 1984; Henwood 1993; see CHAPTER 2, section 2.2.3) each has attempted only to address specific taphonomic issues. The previous investigation demonstrates that taphonomy is more than the study of post-mortem information loss. The actualistic experiments of CHAPTERS 2 and 3 examine the decay and disarticulation of basic insect morphotypes, and relate their breakdown to biogeochemical changes in the tissue. Examination of the biogeochemistry of the Rancho La Brea tar pit insects allows incipient preservation to be further documented (CHAPTER 8). Taken together, the experimental results and examination of the asphalt fossils provide a clearer understanding of the early stages of taphonomy, and are of particular value in the interpretation of other lagerstätten which follow. Each case study examines the processes of preservation in greater detail: authigenic mineralization (CHAPTERS 4, 5, and 7); original organics (CHAPTER 8); altered organics (CHAPTERS 6 and 7); and nodule formation (CHAPTER 4). While the results are, by their nature, pertinent to fossil insects, they are also applicable to other soft-bodied taxa. For that reason, the thesis as a

whole provides a valuable introduction and discussion of the aspects of diagenesis that are so important to our understanding of taphonomy.

9.1.1 Previous models of exceptional preservation

Seilacher (1970) considered the most critical controls on exceptional preservation to be anoxia, rapid burial, and early diagenetic concretion growth, or the occurrence of a particular conservation medium such as asphalt, amber or ice. Seilacher *et al.* (1985) later refined this classification and emphasised obrution, stagnation and cyanobacterial coverings as the key causes of exceptional preservation.

Allison (1988c) considered these earlier schemes to be only loosely causative since only cyanobacterial coverings and rare preservational media such as amber or ice are in any way diagnostic of preservational style. He felt that 'early diagenetic concretions' occur in such a range of circumstances that they cannot be considered diagnostic of causation. Similarly he considered 'obrution' and stagnation' to be primarily palaeoecological in concept. Allison's (1988c) classification scheme was based upon diagenetic mineralization. His scheme concentrated upon three principal factors: rate of burial, salinity and organic content, and how different combinations of these variables function as a precipitation switch, thereby leading to mineral formation.

While Allison's model was a significant advance on those of Seilacher, it still has a number of flaws. The primary focus of the scheme is authigenic mineralization. This fails to take account of organic preservation (hydrocarbon mineralization), which is important in a significant number of deposits. While mention was made of the importance of anoxia and of the anti-bacterial qualities of tannic and fulvic acid in the preservation of soft tissue in the Eocene Geiseltales brown coals (Allison 1988d), no account was given of the preservation of altered organics noted in a number of deposits (*e.g.* Enspel, Messel; see CHAPTER 6). Indeed it is not uncommon to find that certain morphological features are organically preserved, while other parts of the same carcass are mineralized (see CHAPTER 7.3). Allison's classification scheme has since been superseded in at least one area. He claimed that burial was the prime control on pH and therefore the generation of the requisite concentration of phosphate or carbonate required for precipitation. However, the experiments of Briggs and Kear (1993a, 1994b) showed that both phosphatization and calcification can occur in the same carcass where the decay-controlled pH varies. Burial is not the crucial factor.

The following discussion reviews the taphonomy of insects, and documents the factors favouring their preservation. Although the scheme is specific to insects it has broader application to all soft-bodied fossils.

9.1.2 Controls on the preservation of insects

A fossil is the product of all the taphonomic processes that have acted upon it from death to discovery. Decay is perhaps more responsible than any subsequent factor for the resultant morphology of the fossil. Actualistic experimentation has allowed decay thresholds to be identified, so allowing decay inhibition and the onset of mineralization in various fossils to be compared (Briggs and Kear 1993b, 1994a). The rate of decay is controlled by a number of factors including the nature of the organic carbon, temperature and oxidant supply. The factors responsible for decay inhibition are also crucial to the preservation of soft tissue. Anoxia, although it does not prevent decay, reduces the impact of scavengers and microbes, so increasing the longevity of the carcass. Exceptional media, such as asphalt, amber, ice and peat, while responsible for some of the most spectacular preservation, are temporary in nature since decay is inhibited only as long as the specimen remains within the particular encapsulating medium.

However, decay inhibition is not preservation. For fossilization to occur, the tissues must be 'fixed', and that requires either mineralization or organic transformation. In order to preserve labile tissue, such as muscle, mineralization must occur at an early stage. Such mineralization can take place at a resolution of microns and replicate sub-cellular detail. Organic transformation is also important, but it preserves only the more refractory tissue such as cuticle and sclerotized cuticle. Mineralized and organically transformed tissue may subsequently be altered by continued diagenesis.

9.2 DECAY AND DECOMPOSITION

9.2.1 Introduction

Although the utility of experiments in the examination of arthropod taphonomy is firmly established (see Briggs and Kear 1993a, 1994b), those described in CHAPTER 2 represent the first application of the techniques to the study of insects. The experiments are an advance on much of the earlier studies since they relate morphological decay to the biogeochemistry of degradation, so allowing greater quantification of decay. This has the added advantage of facilitating comparison with the fossil record.

In an aerobic system, scavenging and decomposition by sediment microbiota will completely destroy all forms of organic carbon (Okafer 1966a, b; Seastedt and Tate 1981; Seastedt and Crossley 1984; Jørgenson 1983). However, in an anaerobic system, the ability of scavengers and microbes to break down organic carbon is severely impaired and may be completely halted (Jørgenson 1982; Peck and Legall 1982).

9.2.2 Rate of decay

9.2.2.1 Nature of organic carbon. Organic tissue in natural systems is composed principally of the elements C, O, H, N, and P, which occur in variable

proportions and chemical configurations to give a variety of different molecular types. Some molecules, termed volatiles, are rapidly consumed during microbial respiration, while others, termed refractories, are degraded more slowly. Insect soft tissue is proteinaceous and is rapidly decomposed by microbes. The cuticle of insects is composed of a chitin-protein complex which is considerably more refractory.

The experiments of CHAPTER 2 reveal that it is possible to erect a list of insect morphological structures on the basis of their comparative decay resistance (Fig. 9.1). The extreme volatility of the membrane of the heart and other organs, and of muscle tissue, promotes rapid decay-induced information loss. Preservation of these structures requires complete decay inhibition a very early stage. This occurs in exceptional media such as amber and ice, or with the onset of early mineralization.

The cuticle of insects is composed of chitin microfibrils embedded in and intimately linked with a protein matrix (Section 2.7). The cuticle is dominated by protein molecules and it is therefore incorrect to refer to it as composed simply of chitin (Figs. 2.10, 2.11, 8.02). The experiments of CHAPTER 2, and the taphonomic histories discussed in CHAPTERS 5, 7 and 8, indicate that the protein matrix is the most readily biodegraded component. The chitin microfibrils are considerably more refractory. Chitin is particularly refractory where it has undergone sclerotization (Alexander 1973), a process whereby the chitin molecules are strengthened by cross-linking, as in beetle elytra. As the intervening protein matrix is broken down, so the chitin microfibrils are revealed. In helicoidally arranged cuticle, the decay of the matrix produces a 'basket weave'-like appearance. With time the 'vacancies' increase in dimension. The vacancies in sclerotized cuticle, although slower to appear, are ultimately larger than those of non-sclerotized tissue (Figs. 2.10, 2.11). The time frame of cuticle decay is considerably longer than that required for the other tissues of the insect. Consequently cuticle can be preserved both by mineralization and through the organic transformation of the biomolecules to more recalcitrant molecules.

9.2.2.2 Temperature. The microbial degradation of carbon via enzyme-catalyzed reactions is temperature sensitive. The rate of decay increases with temperature to an optimum above which enzymatic reactions become inactive and cell proteins and structures such as membranes are altered. In general, a twofold increase in rate can be expected for a temperature increase of 10°C (Swift *et al.* 1979), although the response of natural microbial communities to temperature changes may vary with season. Other controlling factors may vary with increased temperature, resulting in a three- or fourfold increase in rate (see Payne and King 1972; Bunnel *et al.* 1975; Mason 1983). A decrease in temperature slows decay and when water freezes, a temporary fossil is created. Insects which preserve both muscle tissue and internal organs have been recovered from the

tissue of mammoths preserved in the permafrost of Siberian tundra. As the ice thaws, so decay recommences.

9.2.2.3 Oxidant supply. The most fully understood degradation pathway for organic carbon is that of aerobic respiration, during which organic carbon is combined with oxygen and broken down to yield carbon dioxide and water. However, if the rate of carbon deposition exceeds that of oxygen supply, anoxia results. Anoxia has often been invoked as a decay inhibitor (see Hecht 1933; Zangerl and Richardson 1963; Zangerl 1971). The association of anaerobic conditions with accumulations of sapropelic sediments has generally been accepted as proof that anoxia inhibits decay and is an instrumental factor in the preservation of organic carbon in sediment (*e.g.* Curtis 1980). However, recent experiments on the decay of crustaceans in anoxic mud showed that anaerobic decomposition was rapid, thereby demonstrating that anoxia alone is inadequate to explain the fossilization of soft-parts (Plotnick 1986; Allison 1986). Despite this, comparison of aerobic and anaerobic decay of the cricket (CHAPTER 2) indicate that the latter is considerably slower. Under anoxia some twenty weeks were required for the breakdown of soft-tissue. Even after forty weeks only limited decay was evident, and the cuticle appeared pristine. However, crickets which decayed aerobically showed signs of internal tissue breakdown after only four weeks and were entirely disarticulated by week forty-four. The findings are in accord with the work of Jahnke *et al.* (1982), Benner *et al.* (1984) and Emerson and Hedges (1988). The difference between these findings and those of Plotnick (1986) and Allison (1986), who failed to find any significant decay retardation induced by anoxia, may reflect the nature of organic carbon, *i.e.* the cuticle of the cricket is more refractory than that of crustaceans (see Emerson and Hedges 1988).

Experimentation has shown that under anaerobic conditions, microbes utilize a series of alternative oxidants during decay (*e.g.* manganese, nitrate, iron, *etc.*; see Allison 1988c), in a sequence that is governed by their free energy yield (Allison and Briggs 1993b). In an idealized sediment profile, these reactions are stratified, with decreasing free-energy yields from the top of the pile down (Berner 1981). Consequently anoxia cannot prevent decomposition.

Anoxia inhibits a significant number of scavengers, such as fish, arthropods and worms, all of which can consume a carcass in short order. Anoxia may be the direct result of catastrophic burial, long considered an agent in the preservation of organic soft-parts (*e.g.* Seilacher 1970; Conway Morris 1986) which also distances a carcass from scavengers and bioturbators. Anoxia may also be a crucial factor in a number of 'exceptional' media, such as asphalt, amber and peat (see below).

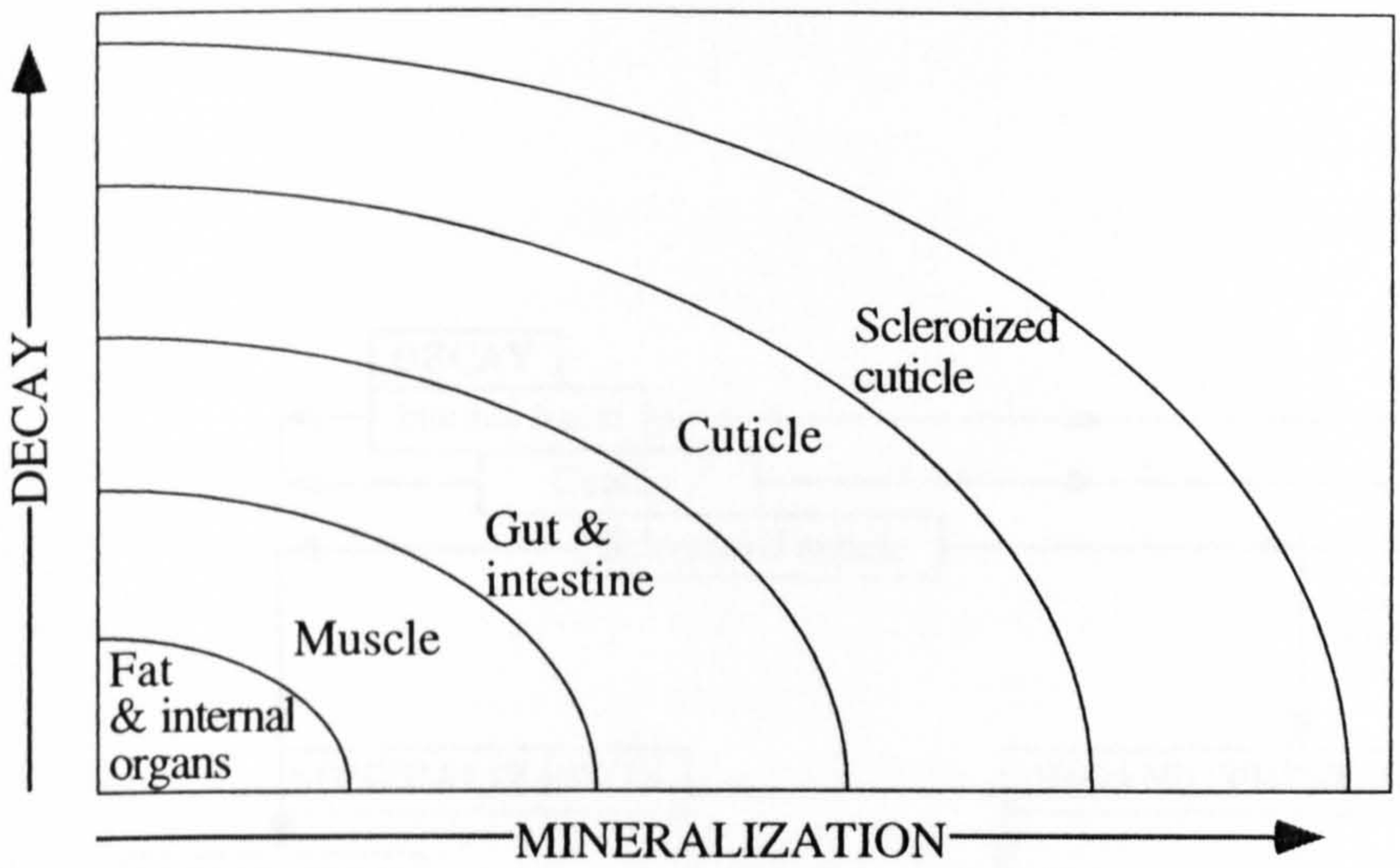


Figure 9.01 Relationship between decay and fossilization in the preservation of insects. Reduced decay and very early minerlization are required for the preservation of labile tissue. If mineralization is impeded and decay continues, only the more refractory elements of the insect will be preserved. (After Allison 1988c).

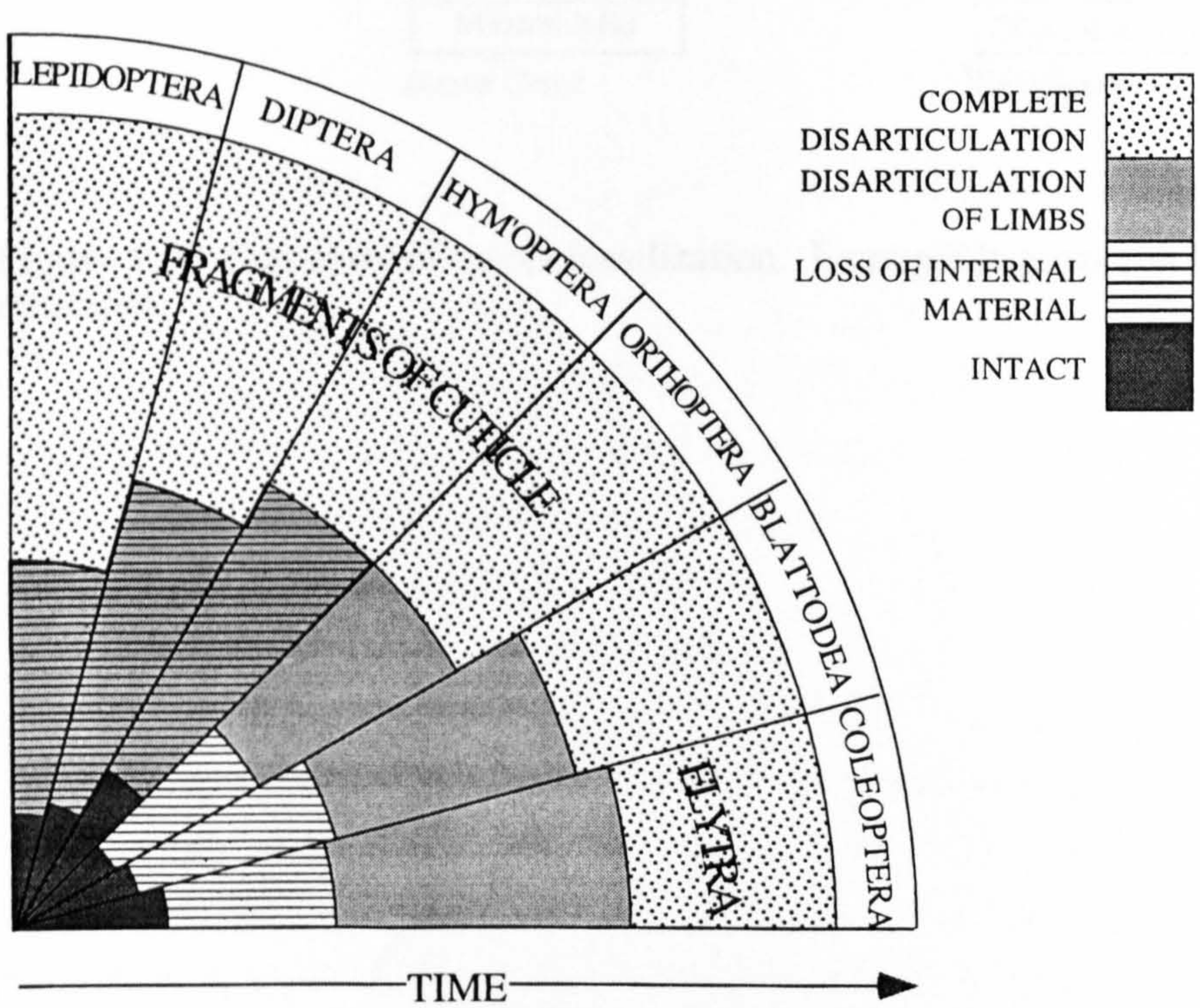


Figure 9.02 Degradation of representative insect orders. The diagram is based upon the results of Chapter 2 (summarised in Fig. 2.09). Only the stages common to all are included. Each boundary represents the first appearance of a particular stage, and not necessarily the termination of the preceding one. Each axis represents the passage of time.

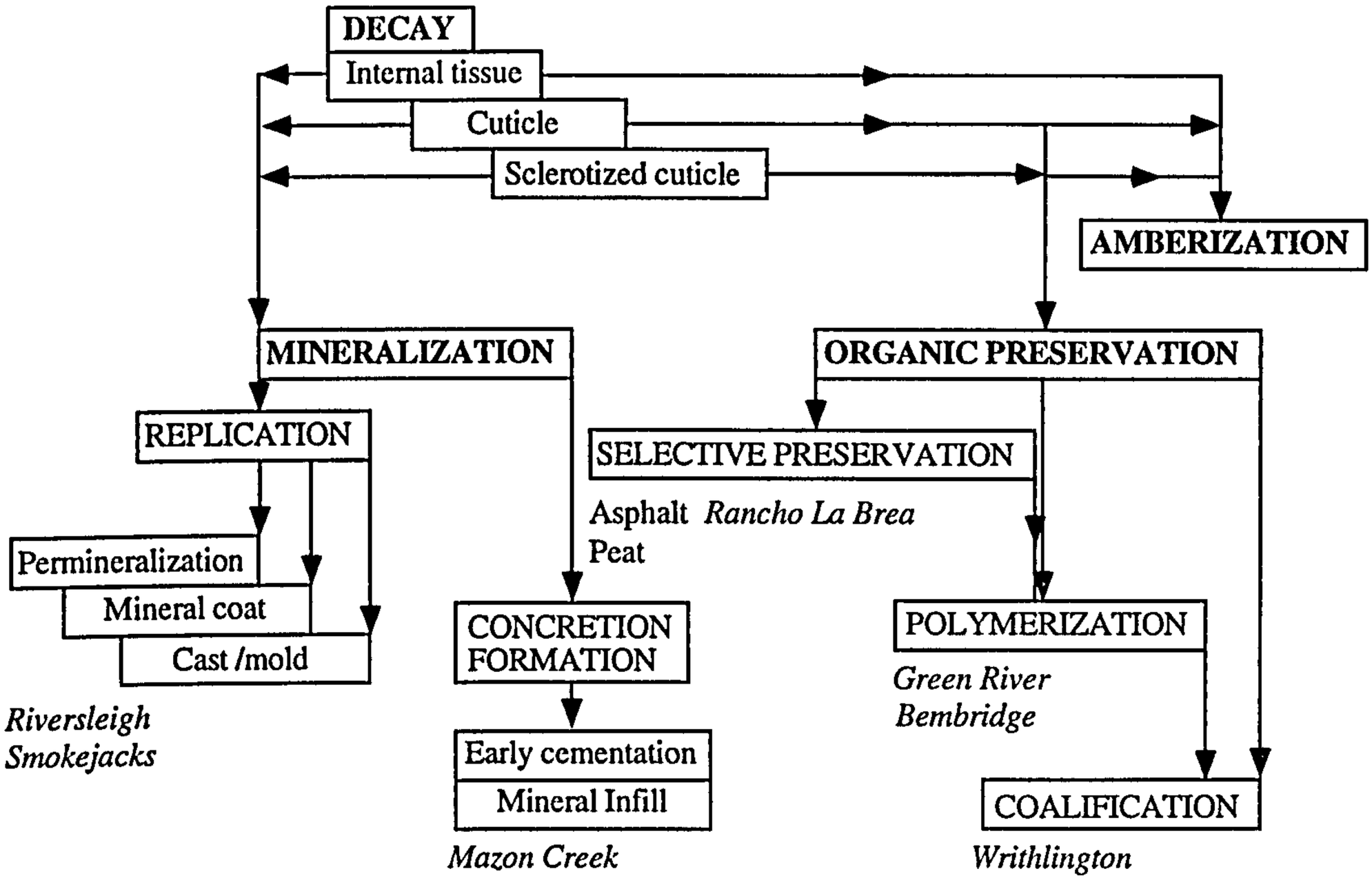


Figure 9.03 Summary of insect fossilization. Example lagerstätten are *italicised*.

9.2.3 Morphological decay

Experimentation (CHAPTER 2) has shown that all insects pass through a broadly similar sequence of decay stages (Figs. 2.09, 2.10, 9.01), only differing significantly in the timing of events. Field-based experimentation suggests that ~6 months are required for complete disarticulation of an insect carcass during the winter and spring months, a period that may well be less in the summer months.

Internal tissue began to breakdown within days of death (Fig. 9.02). After, on average, four weeks, the soft-tissues had decomposed to a state where only small remnants of recognizable structure were evident. This largely structureless material slumped to the bottom of the carcass and was frequently lost from the anal/genital orifices or through ruptures in the arthrodial membrane.

Disarticulation of the abdomen preceded loss of limbs in the field-based experiments, and usually led to buoyancy loss. The last few abdominal segments often disarticulated as a unit, with genitalia attached. The abdomen continued to separate into its constituent segments. In the laboratory based experiments, disarticulation of the abdomen was a much more protracted event.

The detachment and disarticulation of the limbs followed (9.02). The prominent metathoracic legs of certain orders commonly detached at the coxae. The remaining legs, and legs of other orders, disarticulated in a more random fashion, usually from the tarsi torso-ward. Commonly some legs remained attached and articulated after others had become detached.

Disarticulation of the legs always preceded detachment of the wings (9.02). The wings commonly began to fracture along the various veins while still firmly articulated to the thorax. The anal region of blattoid wings commonly disarticulated as a single unit (see also Lutz 1984).

The final stage of disarticulation was the separation of the head from the thorax and the various thoracic segments from one another.

9.2.4 Biochemical breakdown of cuticle

The decay of insect cuticle is protracted (CHAPTER 2). Analysis of experimentally decayed cuticle using flash pyrolysis revealed that the proteins of the endocuticle decay readily, but that the chitin-derived products are relatively refractory (Fig. 2.10, 2.11). The onset of protein decay is reflected by the appearance of vacancies in the endocuticle which increase in size as the protein matrix is destroyed (Plate 2.1 C-F, 2.2 C, D, 2.3 A, B). As the proteins are destroyed, so the chitin microfibrils are gradually revealed. Where the laminae of the endocuticle are helicoidally arranged (see Section 1.4) the decay of protein produces a characteristic basket-weave arrangement of microfibrils (Plate 2.3), a structure evident in fossil insects (CHAPTER 8, Plate 8.1), even where the original chemistry has been highly altered (CHAPTER 7, Plate 7.9). Oblique sectioning of the

cuticle reveals a crescentic arrangement of microfibrils (see Neville 1970, Fig. 5), a feature also noted in fossil cuticle (CHAPTER 5, Plate 5.1D). As the endocuticle decays, the hydrophobic epicuticle does not show any marked structural breakdown (see Plate 2.3 A, B), and is often preserved intact in fossils, even where the endocuticle has experienced decay or complete destruction prior to fossilization (*e.g.* CHAPTER 6, Plate 6.7)

The decay of the sclerotized chitin of the cockroach tegmen (Fig. 2.10) is more limited than that of the beetle elytra (2.11). This may be attributable to the evident difference in the cuticle; cockroach cuticle is leathery and flexible, while beetle cuticle is rigid and brittle. The exact nature of the biochemical control is currently the subject of a study at Bristol University. The more extensive the period of decay, the greater the range of preservational phenomena from temporary fossilization, through early to late stage mineralization, or organic transformation that may replicate the tissue (see below).

9.2.5 Mechanical disarticulation

The experiments of CHAPTER 3 resolve the question of bias in the Carboniferous insect record. In the past, speculation on why cockroach wings dominate to the near exclusion of other body parts has ranged widely. However, these experiments represent the first attempt to resolve the question in a quantifiable sense.

Although reduced transportation has often been cited as a contributory factor in exceptional preservation (see Stürmer and Bergström 1973), the experimental work of Allison (1986) showed that exceptional preservation is no indication of duration and nature of transport. The presence of detached and isolated wings, a common occurrence in the insect record (Carpenter and Burnham 1985), likewise has often been ascribed to extended transport. However, actualistic experimentation (CHAPTER 3) has shown that isolated wings may occur in an assemblage that has not been subjected to extended transport (or for that matter, of decay). Live cockroaches and decayed carcasses rotated in a circular flume experienced neither fragmentation nor widespread disarticulation, as might be expected. The wings do not readily separate, even after extensive decay, and never do so intact. Application of such findings to the cockroaches of Writhlington indicate that neither transport nor decay were responsible for the state of the fossils, suggesting that phenomena such as predation and scavenging may be more important in the production of isolated wings than was hitherto realised.

9.2.6 Future work

The experiments of CHAPTERS 2 and 3 are a valuable first step in the assessment of insect taphonomy. While Henwood (1993) designed experiments to examine only the taphonomy of amber, the decay experiments of CHAPTER 2 were specifically instituted to have the broadest possible application to the insect record. Temperature, water chemistry, and inoculum, were all selected to provide a general sequence of decay, which

could be used in a variety of taphonomic circumstances. The next stage in the development of actualistic analysis, therefore, must be the tailoring of such experiments to particular environmental conditions. For example, the taphonomy of plattenkalks could be investigated by increasing the salinity of the water and utilising a marine bacterial culture; the taphonomy of inland lakes could be examined by utilising freshwater, and a freshwater inoculum. Understanding the variation of particular parameters is only possible when a baseline has been established against which the results can be compared. For that reason, the experiments of CHAPTER 2 are a valuable first step.

Consideration should also be given to variation of decay within taxa. The nature of the experiments described here precluded the documentation of within-order variation. For example, the examination of decay variation across the orders Diptera or Coleoptera could well provide important palaeoecological insights, particularly with reference to the ecology of large water bodies such as the Green River Lakes (CHAPTER 6), or even the Wealden river system (CHAPTER 5). The difference in decay between robust fliers and weak fliers could well have important implications for distance from shore calculations (See Wilson 1984).

Consideration should also be given to such features as the survival of colour in the fossil record, the importance of predation (only touched upon in CHAPTER 3) and the long-term decay of chitin in the cuticle (the experiments of CHAPTER 2 primarily examined the decay of protein). The resolution of such problems and others like them lies in the extension of the techniques and findings of CHAPTERS 2 and 3.

9.3 DECAY TERMINATION

9.3.1 Introduction

While the rate of decay may be slowed (see above), its inhibition is a rare occurrence and requires specific taphonomic circumstances (Fig. 9.03). Decay may be temporarily slowed by encapsulation within certain preservative media: peat, asphalt and amber. However, permanent cessation of information-loss requires diagenesis. In order to preserve volatile tissue such as muscle and organ membrane, mineralization must begin within a matter of weeks. Refractory tissue such as cuticle may be preserved through mineralization, but may also be preserved by transformation of tissues to more recalcitrant molecules.

9.3.2 Temporary fossilization

9.3.2.1 Peat (Fig. 9.03). Peat is one of the most common sources of fossil insects (Elias 1994). Preservation is favoured by the decay resistance of chitin, particularly when cross-linked as in sclerotized cuticle, and the anti-bacterial qualities of tannic and fulvic acids in the peat, which impregnate the carcass and preserve it like tanned leather.

(The sclerotization process is, in itself, a form of tanning). Flash pyrolysis examination of the cuticle of beetles from Quaternary bogs yielded chitin-dominated pyrolyzates, with few protein products (McCobb 1997).

Although no insect volatile tissue has been reported, skin, muscle, and hair of human cadavers and other mammals, has been found (Glob 1969). This may be due to the nature of contact between the peat (and its anti-bacterial waters), and the organism. The soft tissue of endoskeletal organisms is readily impregnated by fluid, whereas the strong, protective exoskeletons of insects with their waxy, hydrophobic epicuticle, is not. Decay within the insect carcass may, therefore, entirely destroy the volatile tissue before it ever comes in contact with the peat's embalming waters.

9.3.2.2 Asphalt (Fig. 9.03). Although asphalt is a comparatively rare preservational medium, the findings of CHAPTER 8 indicate that the examination of such deposits can provide insight into the incipient stages of decay and early preservation. The experiments of CHAPTER 2 were, by necessity, conducted over a very limited period of time. However, examination of material from asphalt deposits, in many ways, provides the missing link between decay and diagenesis. The study has also proved of value in its application of Pyrolysis/Gas Chromatography-Mass Spectrometry to the examination of organic material, with implications beyond asphalt deposits.

The Rancho La Brea site (32,000-6,000 years BP: Marcus and Berger 1984) of California is the most renowned (CHAPTER 8). Examination of the insects revealed that the cuticle is preserved but volatile tissues are entirely absent. The cuticle displays the basket-weave structure of microfibrils characteristic of chitin following protein decay (see above), a fact confirmed by flash pyrolysis. The chitin markers observed in the fossil samples can be easily identified in the pyrograms of modern insect cuticle. However, the protein content is greatly reduced, implying some biodegradation before microbial activity was inhibited by the asphalt. The preservation of certain 'non-chitin' constituents (tyrosine, tryptophan and phenylalanine) indicates at least partial survival of proteinaceous moieties, and implies that these particular amino acids are resistant to degradation.

As in peat, no volatile tissue is preserved, indeed, even the refractory tissues of the bills and talons of birds, and the strong claws of some mammals are absent (Stock 1992). As with peat, preservation is dependent upon the encapsulation and ultimate impregnation of the organism by the preservational medium. However, this process is clearly considerably slower in asphalt. It is likely that much soft tissue of both vertebrates and invertebrates was scavenged and decomposed on the surface by normal aerobic microbial respiration, leaving only the more refractory tissue and biomineralized skeleton. Asphalt, unlike peat, may not have distinct anti-bacterial properties, it may simply create an anaerobic environment free of moisture which prevents microbial activity. Decay by

alternative respiration pathways (see above) would be precluded by the nature of the asphalt medium. Preservation would, therefore, take place in a manner similar to freeze-drying.

9.3.2.3 Amber (Fig. 9.03). Insects preserved in amber are perhaps the most spectacular fossils, with exquisite preservation of the exoskeleton, and internal tissue preserved at a sub-cellular level (see Henwood 1992; Grimaldi *et al.* 1994, Grimaldi 1996) However, claims that DNA has been successfully recovered from amber insects (Cano *et al.* 1992, 1993; DeSalle *et al.* 1992) have recently been questioned (Austin *et al.* 1997). Amber is highly polymerized tree resin; hundreds of deposits occur around the world, varying in age, botanical origin (Langenheim 1969), and the kind and quality of fossil. The best documented are the ambers of the Dominican Republic derived from the *Hymenaea* tree, and of the Baltic region of Europe, derived from a conifer, possibly *Pinus* (Mills *et al.* 1984; Table 1.2). Dominican amber insects are typically perfectly preserved, whereas Baltic specimens have a frothy coating of microscopic bubbles on the body (Mierzejewski 1978), presumably the products of microbial decomposition and/or autolysis of internal tissues (Grimaldi *et al.* 1996). The insect cuticle is structurally intact, although its chemical integrity is unknown. In the insects with preserved tissues, the organs generally show little or no shrinkage (Grimaldi *et al.* 1996), although rarely shrinkage of up to 50% may occur (Henwood 1992). Although muscle tissue is generally intact, the chitinaceous structures of flight muscles are usually better preserved than proteinaceous ones (Grimaldi *et al.* 1996).

The general lack of shrinkage or autolysis, and preservation of volatile tissues, indicate a very rapid and pervasive mummification. Grimaldi *et al.* (1996) claimed such preservation could be facilitated only by the rapid diffusion of the most volatile, low molecular weight fractions in the resin, through the intact body walls (presumably the thin intersegmental membranes) allowing them to perfuse through the tissue, replacing the cellular water. The transparent, light brown halo about some of fossils has been identified as the aqueous body fluids sequestered by the resin (Grimaldi *et al.* 1996). Monosaccharides, alcohols, aldehydes and esters have also been implicated in the process of 'amberization'.

Natural desiccation is also particularly prevalent in new-born and stillborn animals, since they lack a natural gut bacteria (Mason 1983; Janssen 1984; Smith 1986). Indeed, desiccation has long been recognized as a decay inhibitor and was used by the ancient Egyptians and others as a means of preserving the dead. Preservation of these mummies is often exceptional, even at a sub-cellular level (Curry *et al.* 1979; Riddle 1980); cells, albeit shrunken, contain nuclei and nuclear membranes, although mitochondria are rarely observable (Lewis 1967). The linen wrappings of the body were often impregnated with resin, or with pulverized amber (Grimaldi et al. 1996).

9.3.2.4 Future Work. A useful advance on the work of CHAPTER 8 would be a biogeochemical comparison of the insects from various temporary media. While it is commonly assumed that amber fossils are the most intact biochemically (although see Austin 1997), no comparative study has been conducted to compare the preservation of the cuticle of the various deposits: asphalt, amber, peat and ice. Such a study would allow insight into decay termination and the early stages of preservation. Comparison could be extended to see which media best preserve cuticular structure, colour, even muscle. Only by quantifying the cuticle both in terms of chemistry and structure can comparison be legitimately made.

9.3.3 Authigenic mineralization (Fig. 9.03)

9.3.3.1 Introduction. Authigenic mineralization is favoured by anoxia; the removal of oxygen produces a reducing environment and often liberates reactive ionic species (Allison 1988c). The precipitation of these ions as minerals is dependent upon a number of factors including pH, Eh, temperature and relative abundance. The range of tissues types which these minerals may preserve is dependent upon the time at which mineralization begins. To preserve soft-tissue such as muscle, which decays rapidly; mineralization must be rapid. While phosphate is perhaps the most common preserver of muscle tissue (*e.g.* Martill 1990), no phosphatized insect muscle tissue is known. Only goethite (the weathering product of pyrite: P.R. Wilby, *pers. comm.*) has so far been found replicating muscle tissue (*pers. obs.*). More refractory tissue, such as cuticle, may be preserved by a number of minerals, although phosphates and carbonates are amongst the most common. The fidelity of preservation is controlled by the nature of mineralization (permineralization, mineral coat, or cast and mould) and the particular mineral species, which controls crystal form and growth.

This study included three case studies of the action of the phosphate/calcite 'switch': Mazon Creek, USA (CHAPTER 4); the Weald, UK (CHAPTER 5) and Riversleigh, Australia (CHAPTER 7). Each chapter represents an advance in our understanding of the processes of authigenic mineralization. Using the findings of CHAPTERS 2 and 8, it is possible to recognize particular structures in the mineralized material in a manner directly comparable to the results of the actualistic experiments and the examination of the cuticle from Rancho La Brea. The recognition of such features allows a time frame to be placed upon the preservation of material from the three lagerstätten.

The curious finding of this chapter is that mineralization which is known to occur within a matter of weeks in other taxa (Briggs & Kear 1993a, 1994b; Briggs *et al.* 1993), (and indeed it has been speculated that it may occur within a matter of hours: Martill 1989) appears to have taken place only after protracted decay, and only gross morphology is preserved. The question that must therefore be answered is, does

instantaneous mineralization only occur in salt water, or can the experiments of Chapter 2 be refined to produce mineral growth? The answer to the question may lie in the continued examination of fossil insect material under the SEM.

9.3.3.2 Phosphate. Phosphatization is responsible for the highest fidelity of mineralized soft-tissue preservation (*e.g.* Martill 1990; Martill and Wilby 1993; Briggs *et al.* 1993; Wilby and Whyte 1995; Hellmund and Hellmund 1996; Duncan and Briggs 1996). The cuticle of the insects of Riversleigh (Late Oligocene/Early Miocene), Queensland, Australia (CHAPTER 7.1), is preserved on a micron scale, and the ornamentation of the epicuticle and the microfibular arrangement of the endocuticle are evident. Although only the exoskeleton is preserved, this does include the ocular apparatus of some specimens, and the unsclerotized cuticle of larvae. The Wealden insects from Smokejacks (Hauterivian - Barremian), south-eastern England (CHAPTER 5), although less striking in hand specimen, preserve the microfibril arrangement of the endocuticle, in places, at a scale of microns. In both instances, only refractory cuticle is preserved. However, phosphate is known to replicate muscle tissue of vertebrates (Martill 1990), indicating that its precipitation can be very rapid (the so called 'Medusa effect'). The precipitation of apatite about a decaying carcass in the laboratory has constrained this time to a matter of weeks (Briggs and Kear 1993a, 1994b). The absence of volatile tissue in the specimens from Riversleigh and Smokejacks may, therefore, be an indication of advanced decay prior to mineralization (see Fig. 9.1). The phosphatized interior of the Mazon Creek (Westphalian D) insects of the U.S. (CHAPTER 4) is devoid of structure, suggesting that precipitation followed complete destruction of the volatile soft-tissues.

The precipitation of calcium phosphate (apatite) is closely related to that of calcium carbonate (calcite). Indeed the relationship between the two has been likened to a 'switch', with the default set for carbonate (Allison 1988c; Briggs and Wilby 1996). The position of the switch is strongly influenced by microbial activity, which in turn controls the pH and relative concentrations of bicarbonate and phosphate produced as by-products (Berner 1968; Briggs and Kear 1994b; Briggs and Wilby 1996). Experimentation has revealed that phosphatization is favoured by a low pH (Briggs and Kear 1994b) and shown that the switch position need not be static (Briggs and Kear 1994b); tissues initially phosphatized may be overgrown by calcite as the pH rises. This phenomenon, which is almost certainly a factor in the mineralization of the Wealden insects (CHAPTER 5) and those of the Mazon Creek (CHAPTER 4), may reflect exhaustion of the phosphate ion, or a rise in pH with continued decay.

In order to depress the pH and so favour apatite precipitation, the system must be closed. In the case of Riversleigh, this closure may have been facilitated by the presence of algal mats (see Seilacher *et al.* 1985). Indeed, the preservation of the labile larvae may

be a direct result of the intimate association of animal and mat. The growth of concretions about the carcasses at Mazon Creek and the Weald localities may have had a similar effect.

The source of phosphate ions is less certain. The activity of plankton and algae at sites of oceanic up welling are known to concentrate phosphates (Gulbrandsen 1969; Lucas and Prévôt 1984), although this phenomenon clearly cannot be invoked for the preservation of insects, which rarely, if ever, occur in such environments. A more likely scenario is that microbial decay induced mobilization of sufficient phosphate ion to initiate mineralization (Lucas and Prévôt 1985). The death of these microbes quickly results in autolysis and the liberation of enzymes and proto-phosphates. The presence of mineralized microbes intimately associated with the Riversleigh insects (CHAPTER 7.1), indicates that they were petrified before complete autolysis. Such mineralization must occur rapidly after death, and may indeed have caused it.

The *in vivo* precipitation of apatite crystals has also been observed in plaque bacteria (Ennever *et al.* 1981). Microbial decay of surrounding organic material may also liberate phosphate ions. The decay of the surrounding vertebrate soft-tissue at Riversleigh, and the decomposition of the high levels of organic detritus in the river muds of the Mazon Creek and the Weald may have played a crucial role in the production of phosphates. The high concentration of bone was likely an important factor at Riversleigh.

9.3.3.3 Carbonate. Preservation of soft-tissue is more commonly associated with carbonate mineralization than with any other authigenic mineral phase. Under anoxic conditions, the breakdown of organic carbon produces the carbonate ion (Canfield and Raiswell 1991b), commonly calcite (calcium) or siderite (iron).

The calcite/apatite switch may be controlled by pH (see above). At a low pH, apatite is favoured. However, at elevated pHs, the decomposition of carbon produces the bicarbonate ion which can react with the ions of calcium or iron depending upon circumstance (Raiswell 1971, 1976); marine waters are normally saturated with respect to calcium (while the concentration of iron is low) and calcite precipitates, whereas in river-dominated estuaries and deltas, the abundance of iron favours siderite (Berner 1971; Woodland and Stenstrom 1979; Canfield and Raiswell 1991b).

The fidelity of calcite preservation is considerably poorer than that of apatite. While apatite is known to replicate even subcellular details of muscle tissue (Martill 1988, 1990), only the lineations of sarcolemma and muscle fibres were evident in the calcified tissue of the Bembridge insects (CHAPTER 7.3, Plate 7.10F-H; Jarzembowski 1980). The size of the calcite crystals, (in the case of Bembridge, with laths up to 50µm in length), commonly prevents the replication of small scale structures with any fidelity. Indeed, calcified muscle fibres have not yet been reported. Generally only refractory

tissues are preserved, as is evident in the insects of Smokejacks (CHAPTER 5), where only gross structure is preserved in calcite (the microfibrils of the cuticle are preserved in apatite: see above). The Mazon Creek insects (CHAPTER 4) contain not only apatite (see above), but calcite, both equally devoid of structure.

Calcite is more commonly precipitated as a mineral coating on tissue, or replicates tissue as a cast or mould. Although this form of replication is generally poor, exceptional surface detail may be retained, even in the terrestrial environments (Girling 1979). Such preservation is common to plattenkalks (Martinez-Declòs *et al.* 1991, Martinez-Declòs and Martinell, 1993; Wilby *et al.* 1995), and insect-bearing calcareous nodules (Palmer 1957; Park 1990, 1995).

Experimentation has shown that calcification may occur simultaneously with phosphatization in different parts of the same carcass (see Briggs and Kear 1993b), presumably due to within-carcass pH variation. Calcite is also observed to overgrow phosphatized tissue, a feature noted in the fossils of various plattenkalks (Briggs and Wilby 1996).

Siderite is commonly precipitated in fresh/brackish water environments, often in the form of small concretions (CHAPTER 4). Preservation is generally restricted to the traces of particular tissues, which can include the volatile tissue of jellyfish, and the yolk sacs of larval fish (Baird *et al.* 1985a). Amongst the most common fossils are the wings of insects (Carpenter 1938, 1943b, 1944, Carpenter and Richardson 1971; Richardson 1953, 1956).

Siderite is commonly precipitated in concretions. Their formation is clearly favoured by rapid burial and mineral growth. The organic decay of carbon liberates bicarbonate ions (see above), which, in fresh and brackish waters, combine with iron to form siderite. Concretionary growth is controlled by anoxicity, Eh and pH (CHAPTER 4; Berner 1981; Canfield and Raiswell 1991b). Siderite concretions are common in deltaic regions and riverine bogs where the high organic input and rapid burial favour their growth (see Coleman and Ho 1969; Allison and Pye 1994). Recent concretions have been shown to develop over a number of years, although none has yet been found that preserve soft tissue (Allison and Pye 1994). It is therefore likely that the precipitation of siderite at Mazon Creek is at least an order of magnitude faster than that noted in these modern concretions. This process and its mechanism remains unclear.

9.3.3.4 Future work

The examination of phosphatized material from the three localities reveals great variation both in the fidelity of preservation and in the extent of phosphatization. The precipitation of phosphate has been intimately linked to that of calcite in the form of a switch (with the default position set at calcite). The primary control of the switch is

thought to be pH. However, the concept of a 'switch' is almost certainly an over simplification. While it is commonly accepted that calcite cannot be precipitated at low pH (the acid reacts with carbonate to form a salt), there is no necessity to precipitate apatite in its place. A more fundamental control of precipitation is almost certainly the availability of the ions, with pH acting more as a negative filter against calcification than as positive factor in favour of phosphatization. An interesting advance on the experiments of chapter 2, and the work of Briggs and Kear (1993a, 1994b) would be to examine the effects of different tissue type on the end mineral product. The source of ions could be investigated in a similar fashion. In the case of Riversleigh (CHAPTER 7) and possibly the Weald (CHAPTER 5) the source would appear to be the transfer from decaying vertebrate tissue and the degeneration of the bone material. Experiments conducted upon insects in close proximity to rotting carcasses may prove of value.

Perhaps the ultimate advance on the findings of this thesis would be the encouragement of mineralization of insect material. To date, Briggs and Kear (1993a, 1994b) have succeeded only in encouraging mineral growth within shrimps. While this is indeed an impressive feat, the presence of particular salts within the artificial sea water may have acted as an instigator of mineralization. The precipitation of either calcite or apatite within the carcass of an insect in *fresh* water would have far reaching implications for our understanding of much of the fossil record contained within lakes. However, the problem with such an experimental run would almost certainly be the source of ions. Experiments similar to those discussed above using various tissue types or proximity to carcasses may be a way of facilitating mineralization.

The other important finding of the thesis is that phosphatization (and calcification) may play a fundamental role in the preservation of material within siderite nodules. While it is tempting to believe that the absence of phosphatization may hold the key to the difficulty in finding modern analogues of the Mazon Creek nodules, such conclusions must await further study. The findings of CHAPTER 4 are based upon only a limited number of nodules, with examination of the material conducted within strict limits. Therefore, the next step must be the application of the techniques described in the chapter to a wider selection of nodules. Particularly important is the examination of mineralization using elemental mapping. Permission must be secured to section the nodules to facilitate examination of flat surfaces. Serial sectioning through the material would give an insight into the mineral growth stages from core to periphery.

9.3.4 Organic transformation (Fig. 9.03)

9.3.4.1 Introduction. The potential for preservation of biomolecules in the fossil record is generally low and varies with the class of molecules, the depositional

environment, and the diagenetic history (Logan *et al.* 1993). Labile molecules such as nucleic acids and proteins tend to be confined to the temporary preservational media discussed above (although DNA has been reported in leaves from the Clarkia deposit: Golenberg *et al.* 1990). Proteins in cuticles are much more decay resistant (CHAPTER 8). The claim that more recalcitrant biomolecules, such as chitin, are common in the ancient record, often preserved within the cuticles of fine morphological specimens (*e.g.* Carlisle 1964), has been shown to be false (Stankiewicz *et al.* 1997a). While organic remains of insect cuticle are indeed abundant in the fossil record, recent analyses of these fossils have failed to find evidence of the chitin polymer (Stankiewicz *et al.* 1997a), except in Quaternary insects (CHAPTER 8; Miller *et al.* 1983; Stankiewicz *et al.* 1997c) and in beetles from the Oligocene strata at Enspel (Stankiewicz *et al.* 1997b). Excellent preservation of the cuticle morphology is no guarantee of quality preservation of biochemistry. The preliminary control on the preservation of such biomolecules is not time or depositional environment but the inhibition of diagenetic alteration.

The findings of CHAPTERS 6, 7 and 8 represent part of an ongoing study of the biogeochemistry of cuticle conducted at Bristol University. The principal finding of this project is that cuticle is very rarely preserved chemically intact. The common assumption that because a fossil appears brown and lustrous in hand specimen it must preserve chitin is incorrect. The biochemistry of insect cuticle, composed of a chitin-protein complex in life (CHAPTER 1), is invariably highly altered, yielding upon pyrolysis an aromatic or aliphatic polymer characterised by a homologous series of alkanes and alkenes (CHAPTER 7.3; Baas *et al.* 1995; van Bergen *et al.* 1995; Stankiewicz *et al.* 1997a). The cuticle of the 3D Bembridge Marls insects (Eocene), Isle of Wight (CHAPTER 7.3) is a thin organic layer which retains epicuticular ornamentation and internal structure, including layering and the loose 'basket-weave' arrangement of microfibrils indicative of interstitial protein decay (see CHAPTER 2). However, the organic material is aliphatic and retains no original biomolecules. The insects of the Piceance Creek Basin (Palaeocene-Eocene), U.S.A. (CHAPTER 6) are composed of a fine film of amorphous organic material which drapes the underlying matrix. Only in the structures originally sclerotized, such as the elytra and pronota of Coleoptera, is epicuticular ornamentation and internal layering evident.

9.3.4.2 Alteration process. The process whereby the original biomolecules of insect cuticle are converted into more recalcitrant polymers is not yet clear. Although coal, produced by the burial of plant material under reducing conditions, is perhaps the best known source of such altered organic cuticles (*e.g.* Bartram *et al.* 1987; Jarzembowski 1987; CHAPTER 3), it is not the most abundant. In excess of 80% of all organic matter in the fossil record is kerogen (poorly characterized, highly heterogeneous, amorphous, insoluble polymeric material: Logan *et al.* 1993). The composition of

kerogen is dependent upon the source material and the thermal history of the sediment, but its history remains a matter of debate. One hypothesis is that kerogen derives from the condensation products of amino acids and sugars (Durand 1980; Tissot and Welte 1984; CHAPTER 6). An alternative theory is that the most resistant biopolymers derived from algae, terrestrial plants, and soil microbes are selectively enriched relative to more labile (but initially more abundant) biomolecules (see Goth *et al.* 1988; Tegelaar *et al.* 1989; de Leeuw *et al.* 1991; Stankiewicz *et al.* 1997a, b). Macromolecules derived from invertebrate tissues may also be important (Baas *et al.* 1995; Briggs *et al.* 1995; Stankiewicz *et al.* 1997b, c, d in review).

Initially it was postulated that arthropod cuticle could be altered by the replacement with highly aliphatic organic matter from an external plant or algal source (Baas *et al.* 1995). However, a recent study of Carboniferous cuticle found that the distribution and relative abundance of long-chain alkenes/alkanes in the cuticle of arthropods and plants from the same Carboniferous deposit were incompatible with the incorporation of molecular material from plant into arthropod cuticles during diagenesis (Stankiewicz *et al.* 1997d). Thus the alteration could not be produced by random re-polymerization of organic matter in sediment, but only through polymerization *in situ*, within the cuticles.

The only aliphatic substances found in insects are the lipids or waxes of the epicuticle (5% of cuticular mass: Kolattukudy 1976). Polymerization of the non-waxy constituents that form the bulk of the cuticle would result in the loss of structure while polymerization of the remaining waxy constituents would produce the aliphatic signature (Stankiewicz *et al.* 1997d, in review; CHAPTER 6). However, the destruction of the original chemistry of the cuticle need not imply destruction of its morphology (see CHAPTER 7.3; Bartram *et al.* 1987; Schaal and Ziegler 1988; Stankiewicz *et al.* 1997a). The resolution of this problem is presently the subject of an intensive study at Bristol University (see Stankiewicz *et al.* 1996, 1997a, b, c, d in review, e in review).

9.3.4.3 Future work

The Bristol group continue to examine preservation of cuticle in the fossil record. Recent work (Stankiewicz et al. 1997e) has already precluded the possibility that the aliphatic/aromatic signature is the result of the transference of molecules from adjacent plant material (as envisaged by Baas et al. 1995). However, a definitive explanation of the phenomenon has not yet been found.

Future work should examine the entire spectrum of organic preservation from chemically and structurally intact fossils (e.g. those in peat or asphalt), through those which are structurally intact but chemically altered (e.g. Bembridge insects) to those which are both structurally and chemically altered (e.g. insects preserved in kerogen and coal). The examination of material preserved in coals which has not yet undergone lithification may prove of value. However, one of the problems of examining fossil

material preserved in kerogen or coal is that the utility of py-GC/MS is reduced because of the risk of contamination by the surrounding matrix.

9.4 CONCLUSION

To understand the bias in the fossil record one must first understand taphonomy, since what is found in any Lagerstätte is controlled by preservation. The richness of the Quaternary and Tertiary insect record (see Labandeira and Sepkoski 1993; Jarzembowski and Ross 1993), is a result of the number lagerstätten, but more importantly, the wide variety of preservational styles surviving from these periods compared to others. Since each type of preservation introduces some form of bias no matter how impressive the fossils may appear (*e.g.* amber is inherently biased against insects which occupy the herbage and soil layers: Henwood 1993), the greater the range of styles of preservation, the more complete will be our understanding of any period. For example, although Carboniferous insects are known primarily from coal-bearing deposits, the insects of the relatively uncommon siderite concretions significantly enhance the record. The information preserved by two styles or more provides as more complete understanding of the record.

The aim of this project was to assess the quality of information retained by the main styles of preservation. Such information allows the broader questions raised by the fossil record of insects to be answered. Why are there significant gaps in the history of the insects? What impact has mass extinction had on the insect record? The answers to such questions requires a sound understanding of taphonomic principles. The ultimate aim of this project, and taphonomy in general, is to provide information which allows the fidelity of fossilization and range of taxa present to be related to particular preservational mechanisms, thereby producing a powerful tool which can be used to assess any lagerstätten.

APPENDIX 1

ANALYTICAL TECHNIQUES

A1.1 SCANNING ELECTRON MICROSCOPE (SEM)

1.1.1 Introduction

The scanning electron microscope (SEM) allows the collection of high magnification/high resolution images (see Goldstein *et al.* 1981, Taylor 1986). The imaging process involves beaming a narrow stream of electrons across the surface of a specimen to produce a number of secondary electrons (SEs). These SEs are produced from inelastic events which transfer energy from beam to specimen, producing a 'photographic' image. Contemporaneous with the emission of SEs, the specimen itself produces high energy emissions known as back scatter electrons (BSEs) which result from elastic events where no energy is transfered between beam and specimen (Taylor 1986). The backscatter electron image emphasizes mineral variation within the scanned material. The electrons emitted in this fashion are collected by an electron detector, processed and displayed on a cathode ray tube with a visible raster synchronized to the beam scan.

Electrons are produced by heating a tungsten filament housed within a cathode assembly held at a high accelerating voltage, to approximately 2300°C. By varying the accelerating voltage, the speed of the electrons and wavelength of the electron beam can be altered. The electron column through which the beam passes, is held under a high vacuum which allows unhindered passage of the electrons and reduces high voltage discharge.

1.1.2 Method

All specimens were examined using a Cambridge scanning electron microscope at 7-10kV for modern insect cuticle and 10-15kV for fossil material. The modern cuticle was freeze-dried for 12 hours prior to examination. All material was mounted on aluminium stubs using carbon tape or silver dag, and coated in gold (or carbon, when specimens were subsequently to be examined under the electron microprobe).

A1.2 ELECTRON MICROPROBE ANALYSIS

1.2.1 Introduction

The electron microprobe can used to characterise the elemental make-up of a fossil. The basic process of X-ray production is essentially similar to that described for the production of SEs above, with the emission of X-rays whose energy and abundance are dependent upon the composition of the sample (see Goldstein *et al.* 1981). By measuring the wavelengths and energies of these x-rays, the elements can be ascertained. By measuring the intensities of the x-rays and comparing them to sets of known standards, a quantitative determination of the elements present can be obtained.

The microprobe can produce both standard scanning electron images, and backscatter images which together indicate variations in fossil topography and mineralogy. This

information allows regions of interest, or potential mineral variation, to be determined and the elemental make-up to be examined. The most accurate analyses result from the examination of polished surfaces, since the relief of an unpolished specimen may distort the beam reflection producing erroneous results, a phenomenon termed the topographic effect.

The electron microprobe also permits elements to be mapped relative to one another, so allowing the relationship of diagenetic minerals to be examined in a non-destructive fashion (see Martill *et al.* 1992). The initial step requires the selection of the elements considered likely to be present. This may be achieved by reading the literature related to the biota, or by examination of the fossil using the microprobe (as described above). The region to be mapped must be delineated. The highest quality results are produced from polished slabs (see above). Unfortunately, this process is destructive and permission is not always granted by lending institutions. However, unpolished specimens with limited relief can produce significant results. The electron beam analyses the fossil in a series of traverses. When viewed together these traverse form an elemental map

1.2.2 Method

All specimens were examined using a Jeol JXA superprobe (operating conditions: 15kV; 5nA; spot size - 10μm). All specimens were examined unpolished (as a result of restrictions imposed by the various museums). In order to reduce topographic effect regions of low relief were, whenever possible, selected for examination. The specimens were carbon coated.

A1.3 X-RAY DIFFRACTION

1.3.1 Introduction

X-ray diffraction provides a qualitative and quantitative assessment of the mineralogy of rock and fossil material. Since each mineral is defined by a crystal lattice with characteristic diffraction properties it can be resolved by x-rays. The Ångstrom d-spacing of certain crystallographic lattice directions show up as relative peak (area) heights on the diffractogram in a fixed relationship. Using calibrated peak-area intensities of the major peak, the proportion in a profile can be given with about ±5% at for minerals which constitute more than 5% of the bulk sample.

The x-ray diffractometer consists of an x-ray source, a movable sample platform, an x-ray detector and associated computer controlled electronics. Material to be examined is ground to a grain size of ~100μm, mixed with acetone and deposited as a slurry onto a glass cover slip. The sample is placed in a holder which spins slowly during analysis to reduce sample heating. The source of the x-ray is a copper anode. The x-ray beam is fixed and the sample platform rotates with respect to the beam by an angle of theta. The

detector rotates at twice the rate of the sample and is at an angle of 2-theta with respect to the incoming x-ray beam.

1.3.2 Method

All material was examined using Phillips PW 1800 X-ray Diffractometer (operating conditions (45kV; 40mA; Cu anode). Material was carefully excavated from the appropriate sample and ground to a powder (~100µm). This powder was mixed with acetone, and the slurry deposited on a glass cover slip to a thickness of ~0.5mm.

A1.4 PYROLYSIS-GAS CHROMATOGRAPHY/MASS SPECTROMETRY (Py-GC/MS)

1.4.1 Introduction

This technique combines separation of chemical compounds using gas chromatography and their subsequent identification using mass spectrometry. It is particularly valuable technique since only minute quantities of organic material (<1mg) are required for analysis. The techniques allow very rapid screening of complex materials. For a full discussion of the technique, see Stankiewicz et al. 1996 and references therein.

1.4.2 Method

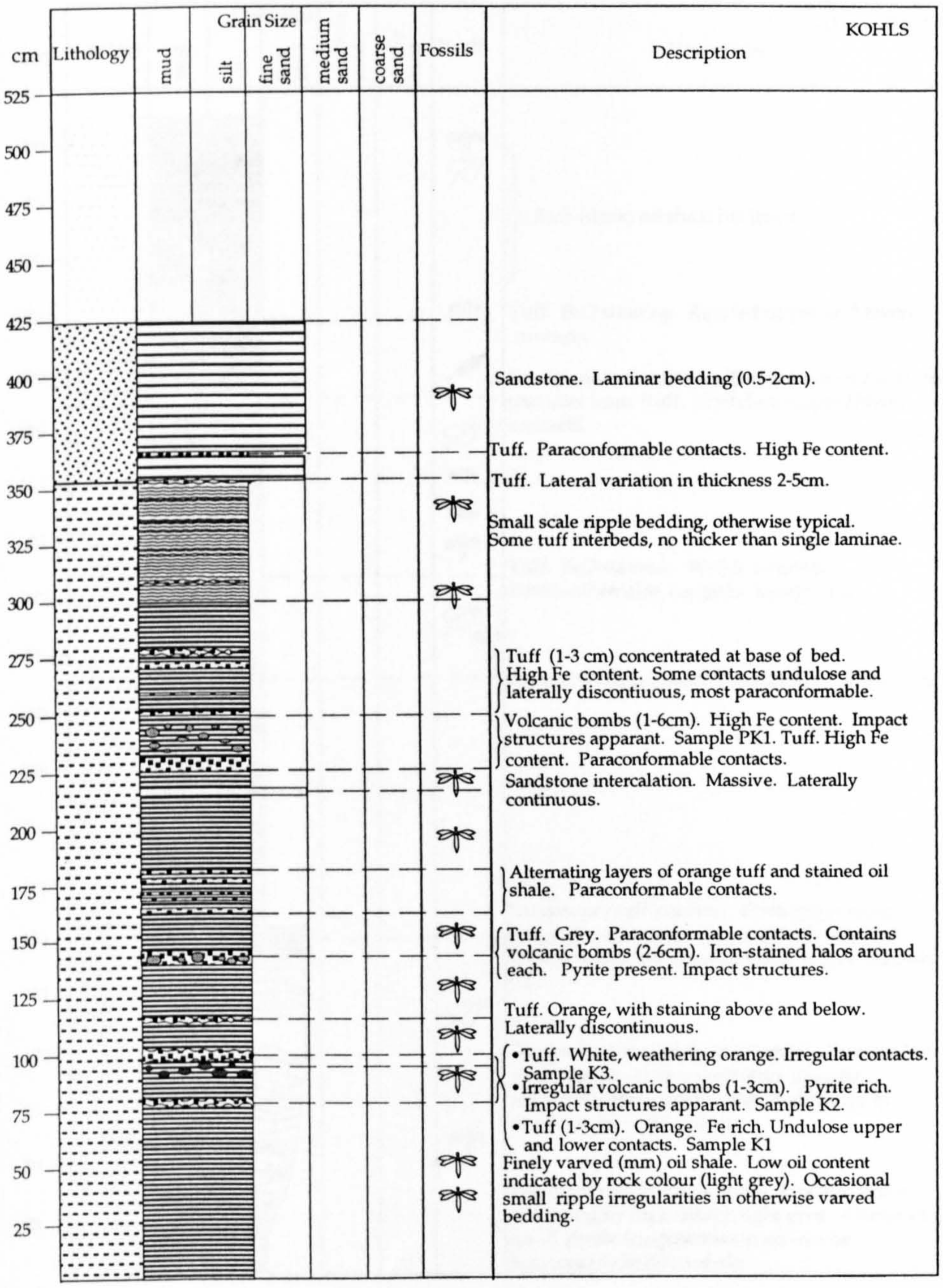
Specimens are first freeze-dried to remove all moisture for a period not less than 12 hours. They are then solvent extracted to remove contaminents using dichloromethane and methanol in the ratios 1:1, 2:1 and 1:0 in sequence. Between each addition of solvent, the specimens were sonicated in a water bath.

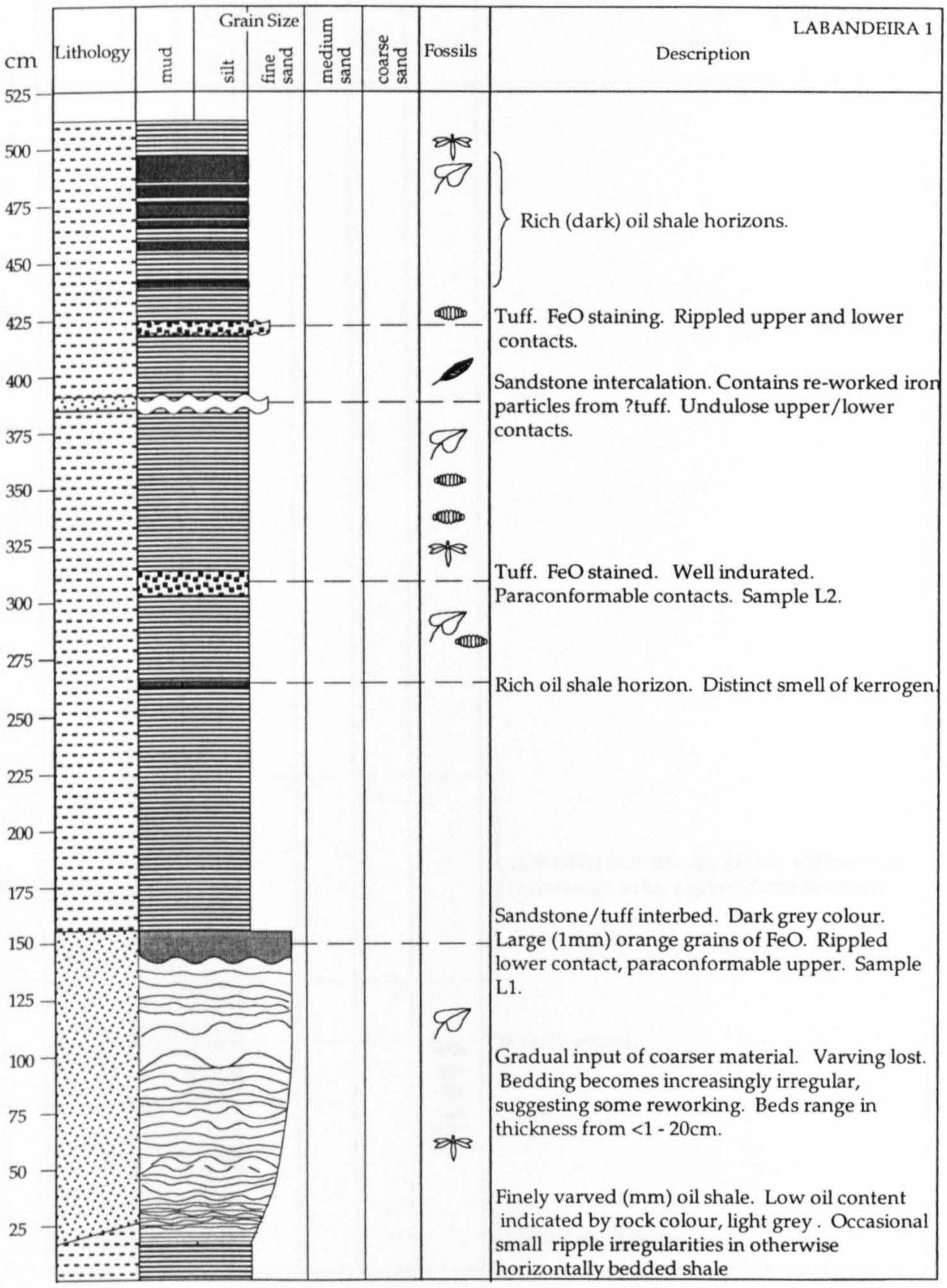
The solvent extracted cuticle is weighed (*ca* 0.1 mg of each sample) and placed in a quartz sample holder. It is then pyrolysed in a flow of helium for 10 seconds in a platinum coil at 610°C using a Chemical Data System 1000 pyroprobe coupled to a Carlo Erba 4130 GC interfaced with a Finnigan 4500 MS. Compounds are separated using a Chrompack CP Sil-5 CB column (50 m x 0.32 mm i.d., film thickness 0.4 µm; dimethyl polysiloxane equivalent). The GC oven is operated as follows: isothermal for 5 minutes at 35°C; temperature programmed at 4°C/min. to 315°C and then isothermal for 15 minutes. The MS was operated in full scan mode (40-650 daltons, 1 scans/sec., 70 eV ionisation voltage). Peaks are identified based on their mass spectral characteristics and GC retention indices, by comparison with authentic chitin (Aldrich, U.K.), chitosan, peptides and amino acid standards (Stankiewicz *et al.*1996) and with reference to the literature (van der Kaaden *et al.*, 1984; Franich *et al.*, 1984).

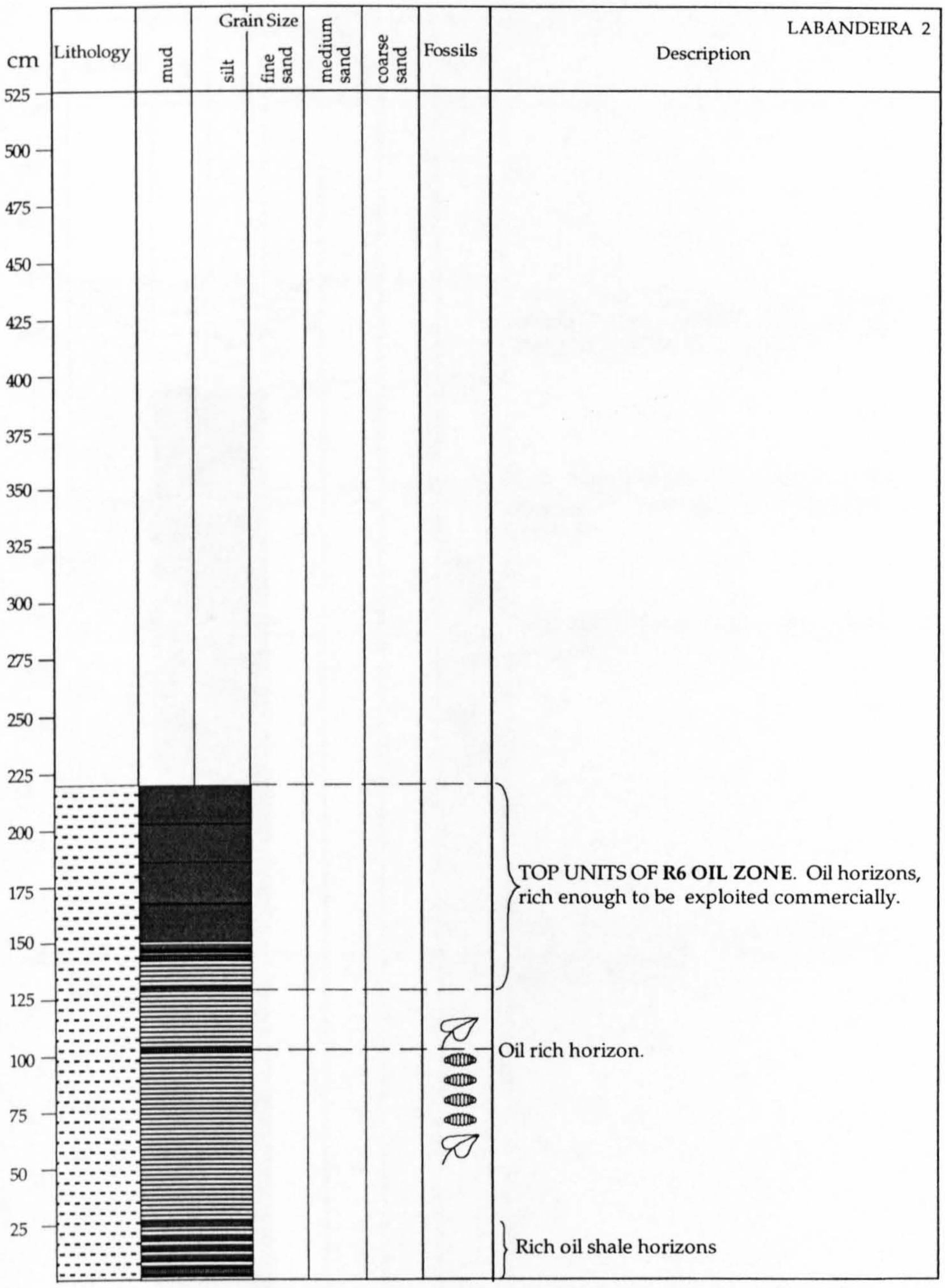
APPENDIX 2.1

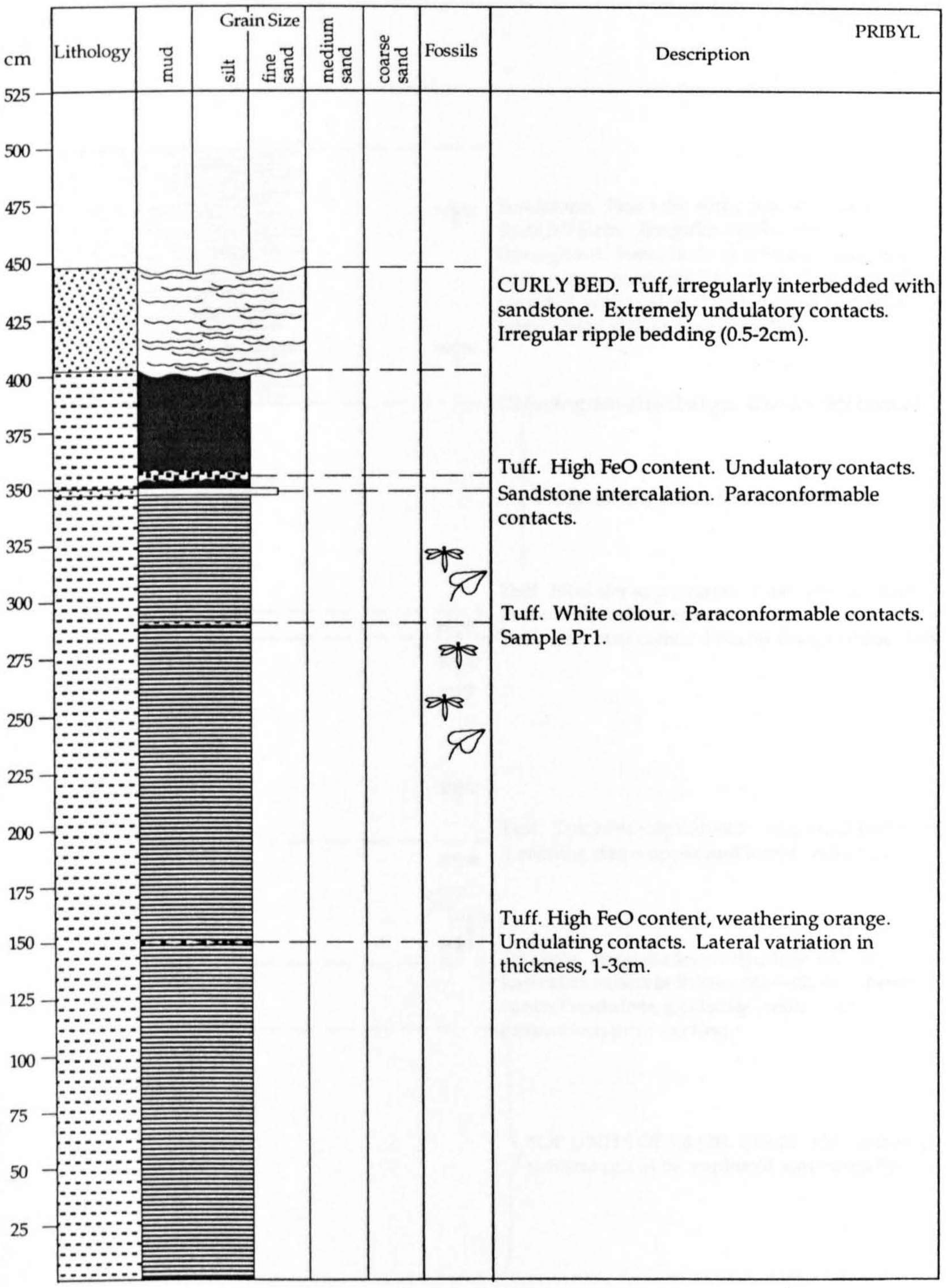
GRAPHIC LOGS
PICEANCE CREEK BASIN

(Location details in the possession of the author)

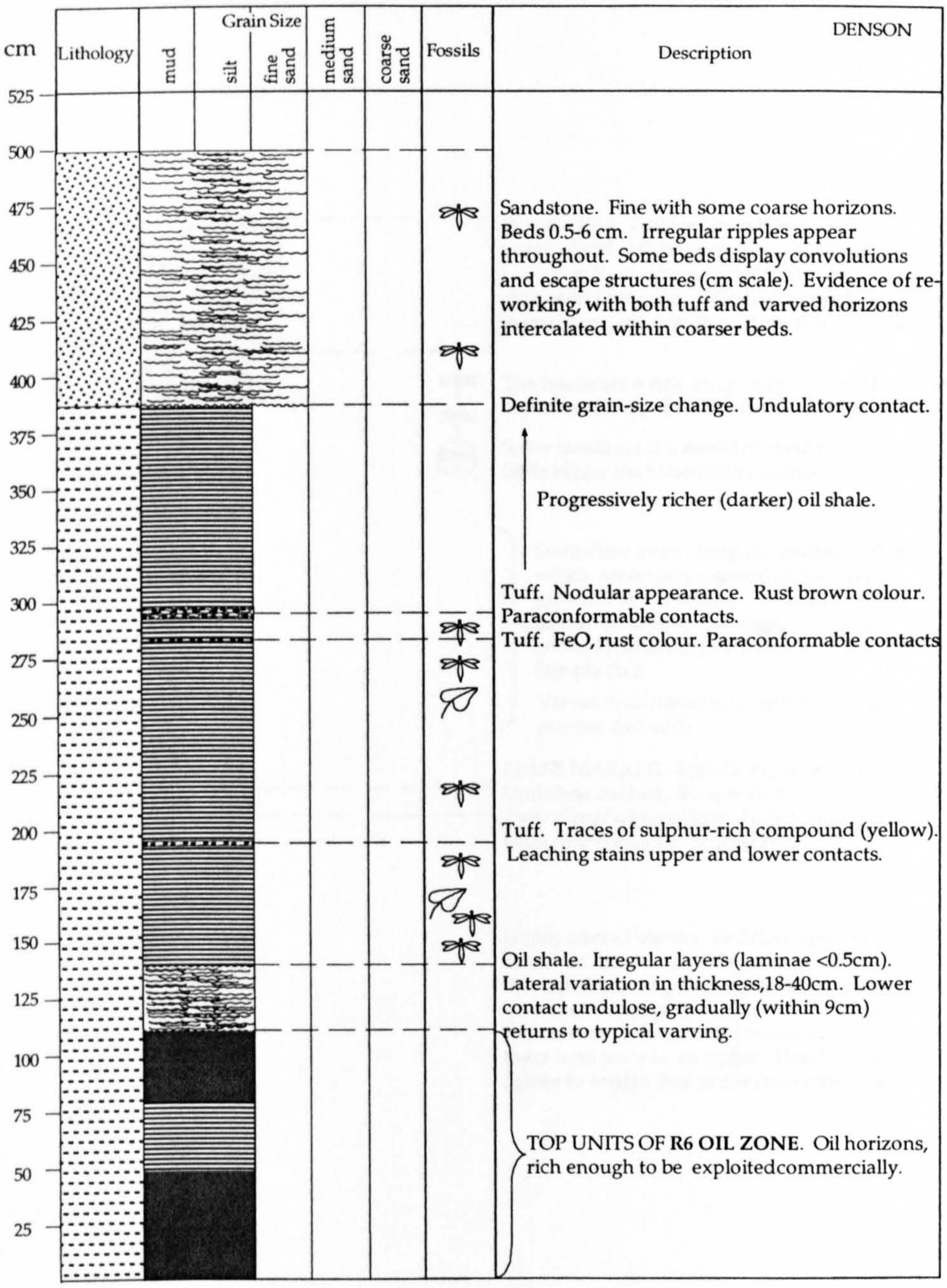

KOHLS
cm
Lithology
mud
Grain Size
silt
fine sand
medium sand
coarse sand
Fossils
Description
525
500
475
450
425
400
375
350
325
300
275
250
225
200
175
150
125
100
75
50
25
Sandstone. Laminar bedding (0.5-2cm).
Tuff. Paraconformable contacts. High Fe content.
Tuff. Lateral variation in thickness 2-5cm.
Small scale ripple bedding, otherwise typical.
Some tuff interbeds, no thicker than single laminae.
Tuff (1-3 cm) concentrated at base of bed.
High Fe content. Some contacts undulose and
laterally discontiuous, most paraconformable.
Volcanic bombs (1-6cm). High Fe content. Impact
structures apparant. Sample PK1. Tuff. High Fe
content. Paraconformable contacts.
Sandstone intercalation. Massive. Laterally
continuous.
Alternating layers of orange tuff and stained oil
shale. Paraconformable contacts.
Tuff. Grey. Paraconformable contacts. Contains
volcanic bombs (2-6cm). Iron-stained halos around
each. Pyrite present. Impact structures.
Tuff. Orange, with staining above and below.
Laterally discontinuous.
•Tuff. White, weathering orange. Irregular contacts.
Sample K3.
•Irregular volcanic bombs (1-3cm). Pyrite rich.
Impact structures apparant. Sample K2.
•Tuff (1-3cm). Orange. Fe rich. Undulose upper
and lower contacts. Sample K1
Finely varved (mm) oil shale. Low oil content
indicated by rock colour (light grey). Occasional
small ripple irregularities in otherwise varved
bedding.

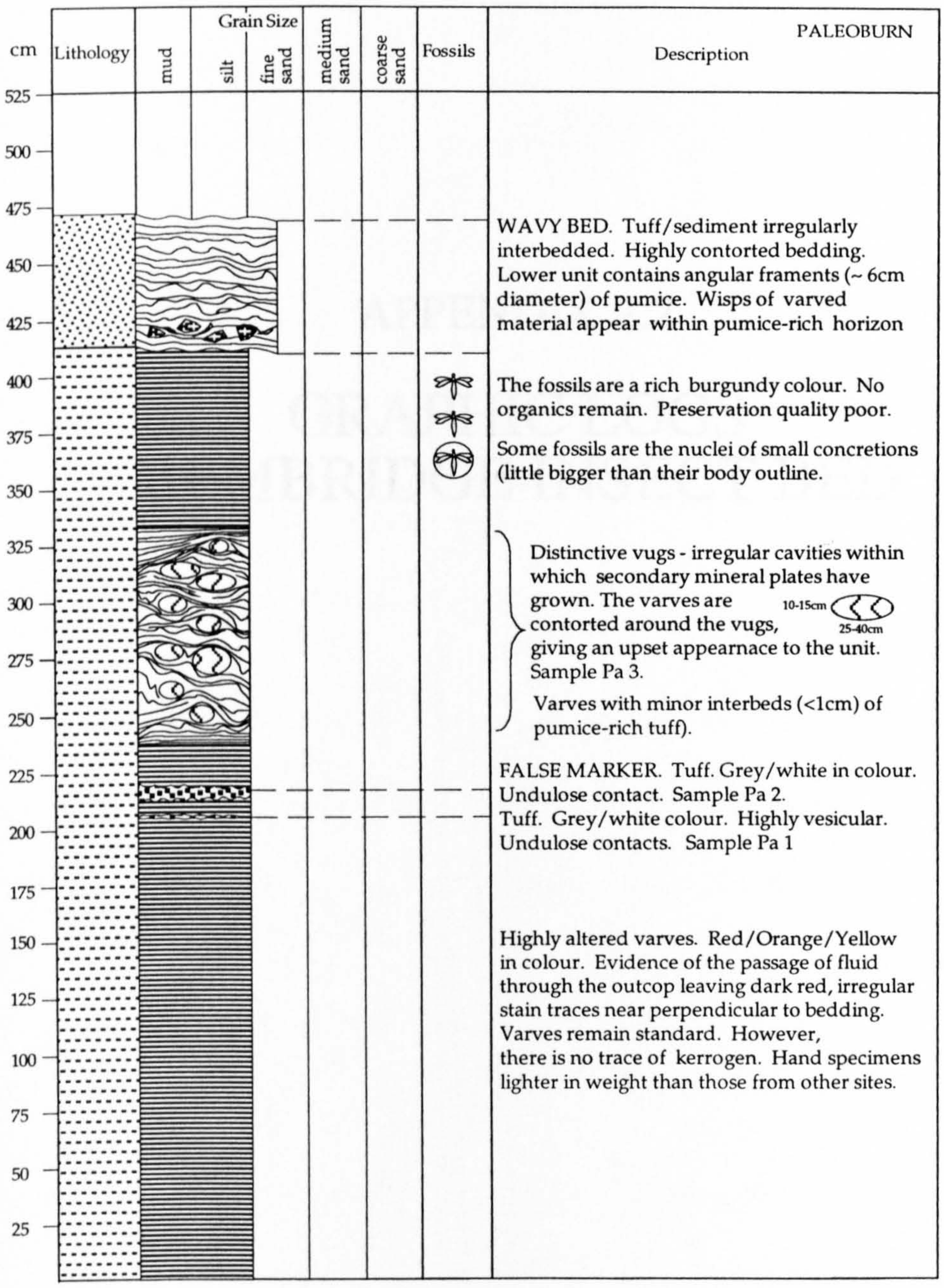

LABANDEIRA 1
cm
Lithology
Grain Size
mud
silt
fine sand
medium sand
coarse sand
Fossils
Description
525
500
475
450
425
400
375
350
325
300
275
250
225
200
175
150
125
100
75
50
25
Rich (dark) oil shale horizons.
Tuff. FeO staining. Rippled upper and lower contacts.
Sandstone intercalation. Contains re-worked iron particles from ?tuff. Undulose upper/lower contacts.
Tuff. FeO stained. Well indurated. Paraconformable contacts. Sample L2.
Rich oil shale horizon. Distinct smell of kerrogen.
Sandstone/tuff interbed. Dark grey colour. Large (1mm) orange grains of FeO. Rippled lower contact, paraconformable upper. Sample L1.
Gradual input of coarser material. Varving lost. Bedding becomes increasingly irregular, suggesting some reworking. Beds range in thickness from <1 - 20cm.
Finely varved (mm) oil shale. Low oil content indicated by rock colour, light grey . Occasional small ripple irregularities in otherwise horizontally bedded shale


LABANDEIRA 2
cm
Lithology
mud
Grain Size
silt
fine sand
medium sand
coarse sand
Fossils
Description
525
500
475
450
425
400
375
350
325
300
275
250
225
200
175
150
125
100
75
50
25
TOP UNITS OF R6 OIL ZONE. Oil horizons, rich enough to be exploited commercially.
Oil rich horizon.
Rich oil shale horizons
Top of Labandeira 1


cm
Lithology
mud
Grain Size
silt
fine sand
medium sand
coarse sand
Fossils
Description
PRIBYL
525
500
475
450
425
400
375
350
325
300
275
250
225
200
175
150
125
100
75
50
25
CURLY BED. Tuff, irregularly interbedded with sandstone. Extremely undulatory contacts. Irregular ripple bedding (0.5-2cm).
Tuff. High FeO content. Undulatory contacts.
Sandstone intercalation. Paraconformable contacts.
Tuff. White colour. Paraconformable contacts.
Sample Pr1.
Tuff. High FeO content, weathering orange. Undulating contacts. Lateral vatriation in thickness, 1-3cm.

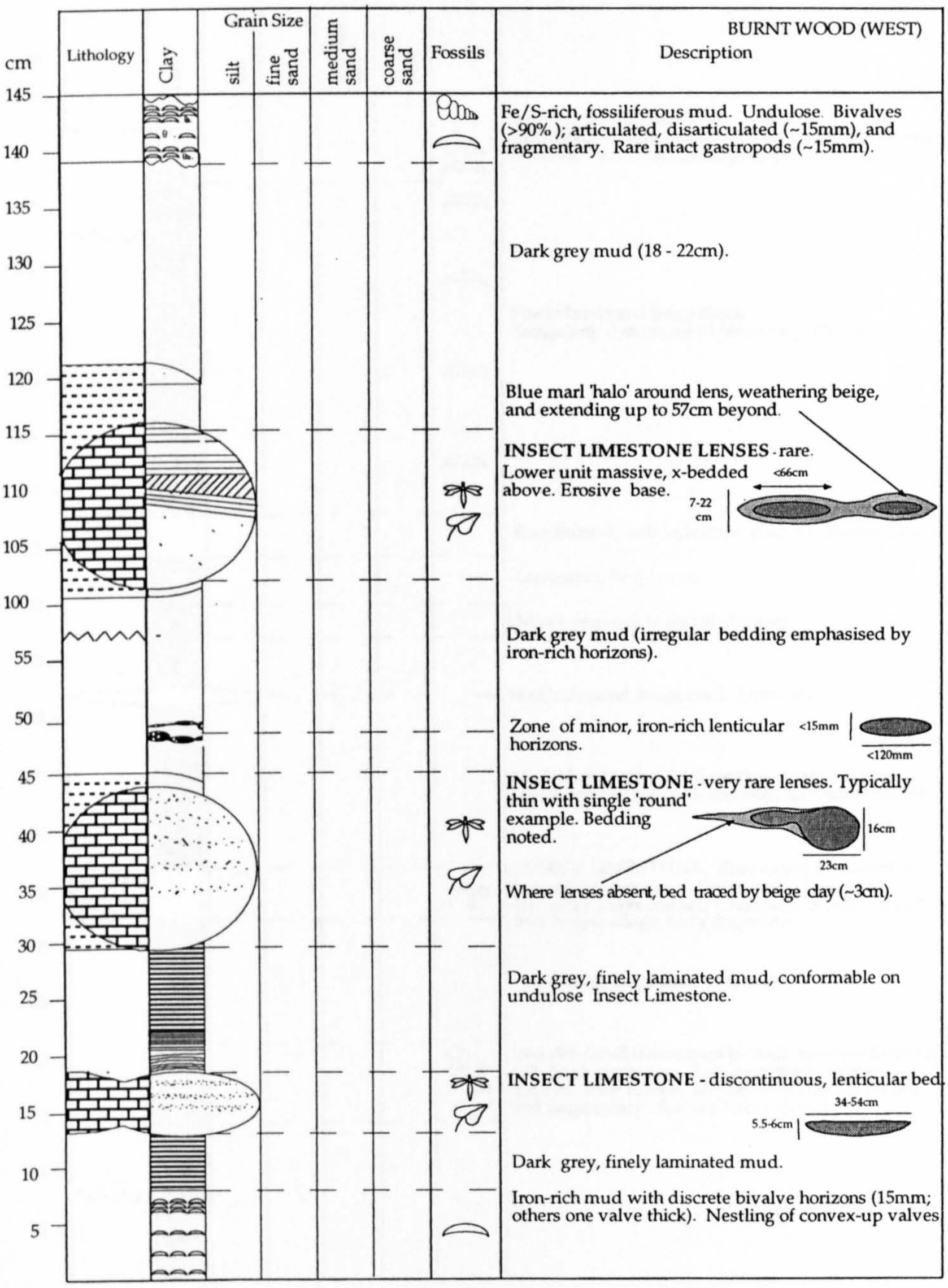
DENSON

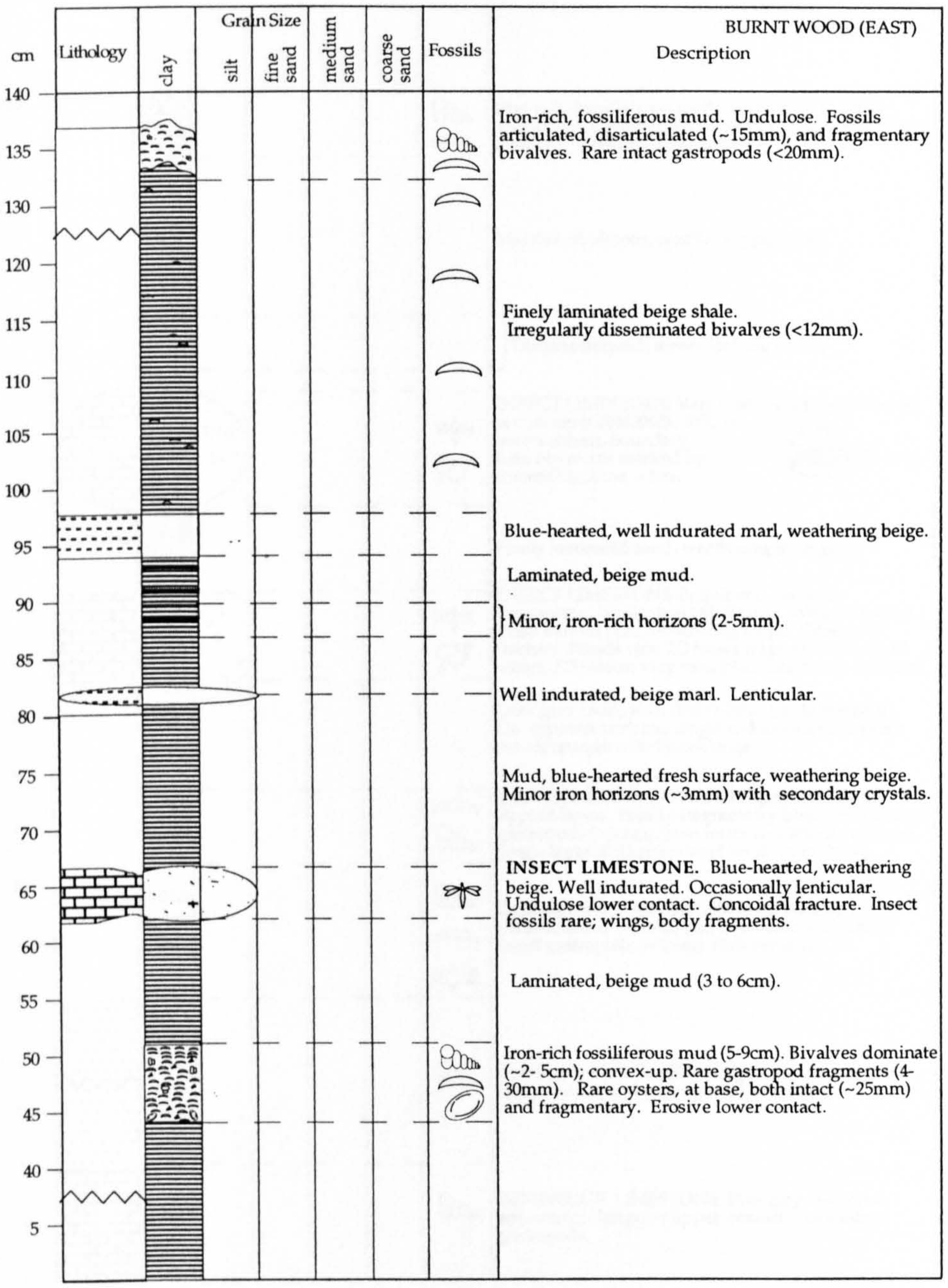

cm
Lithology
Grain Size
mud
silt
fine sand
medium sand
coarse sand
Fossils
Description
525
500
475
450
425
400
375
350
325
300
275
250
225
200
175
150
125
100
75
50
25
Sandstone. Fine with some coarse horizons. Beds 0.5-6 cm. Irregular ripples appear throughout. Some beds display convolutions and escape structures (cm scale). Evidence of re-working, with both tuff and varved horizons intercalated within coarser beds.
Definite grain-size change. Undulatory contact.
Progressively richer (darker) oil shale.
Tuff. Nodular appearance. Rust brown colour. Paraconformable contacts.
Tuff. FeO, rust colour. Paraconformable contacts
Tuff. Traces of sulphur-rich compound (yellow). Leaching stains upper and lower contacts.
Oil shale. Irregular layers (laminae <0.5cm). Lateral variation in thickness,18-40cm. Lower contact undulose, gradually (within 9cm) returns to typical varving.
TOP UNITS OF R6 OIL ZONE. Oil horizons, rich enough to be exploitedcommercially.

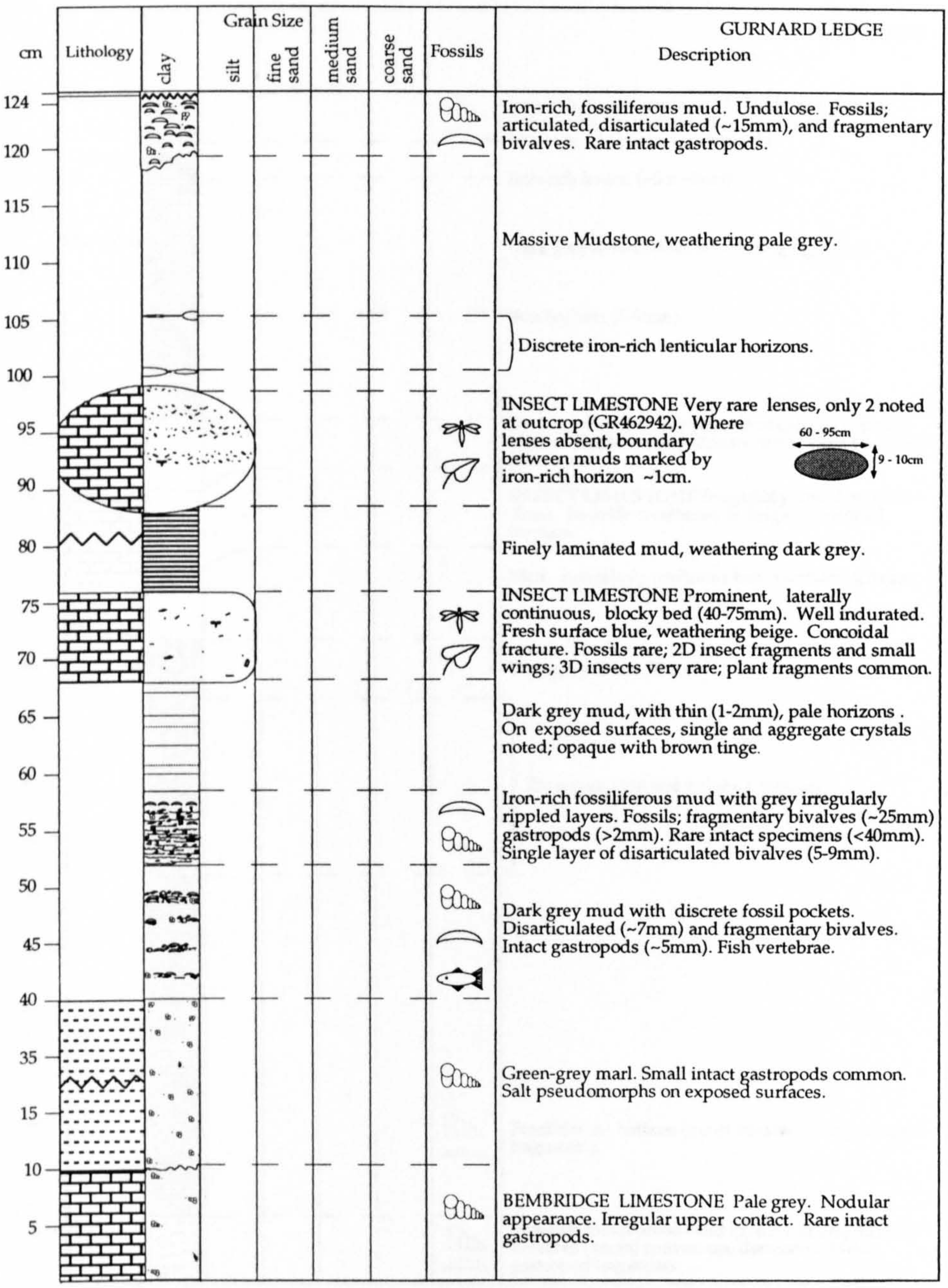

PALEOBURN
cm
Lithology
Grain Size
mud
silt
fine sand
medium sand
coarse sand
Fossils
Description
525
500
475
450
425
400
375
350
325
300
275
250
225
200
175
150
125
100
75
50
25
WAVY BED. Tuff/sediment irregularly interbedded. Highly contorted bedding. Lower unit contains angular framents (~ 6cm diameter) of pumice. Wisps of varved material appear within pumice-rich horizon
The fossils are a rich burgundy colour. No organics remain. Preservation quality poor.
Some fossils are the nuclei of small concretions (little bigger than their body outline.
Distinctive vugs - irregular cavities within which secondary mineral plates have grown. The varves are contorted around the vugs, giving an upset appearnace to the unit. Sample Pa 3.
10-15cm
25-40cm
Varves with minor interbeds (<1cm) of pumice-rich tuff).
FALSE MARKER. Tuff. Grey/white in colour. Undulose contact. Sample Pa 2.
Tuff. Grey/white colour. Highly vesicular. Undulose contacts. Sample Pa 1
Highly altered varves. Red/Orange/Yellow in colour. Evidence of the passage of fluid through the outcop leaving dark red, irregular stain traces near perpendicular to bedding. Varves remain standard. However, there is no trace of kerrogen. Hand specimens lighter in weight than those from other sites.

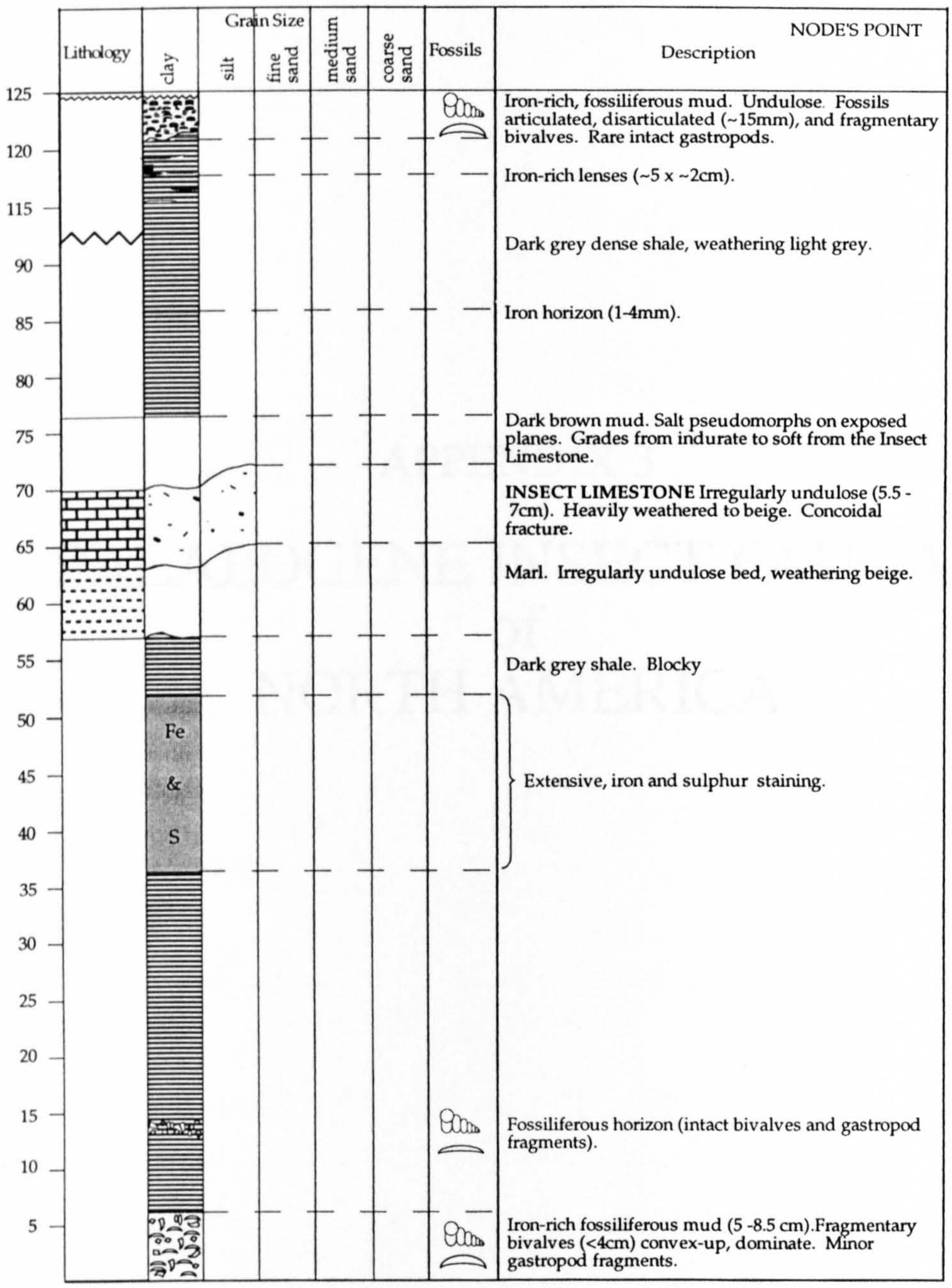
APPENDIX 2.2

GRAPHIC LOGS
BEMBRIDGE INSECT BED


BURNT WOOD (WEST)
cm
Lithology
Clay
Grain Size
silt
fine sand
medium sand
coarse sand
Fossils
Description
145
140
135
130
125
120
115
110
105
100
55
50
45
40
35
30
25
20
15
10
5
Fe/S-rich, fossiliferous mud. Undulose. Bivalves (>90%); articulated, disarticulated (~15mm), and fragmentary. Rare intact gastropods (~15mm).
Dark grey mud (18 - 22cm).
Blue marl 'halo' around lens, weathering beige, and extending up to 57cm beyond.
INSECT LIMESTONE LENSES - rare.
Lower unit massive, x-bedded above. Erosive base.
<66cm
7-22 cm
Dark grey mud (irregular bedding emphasised by iron-rich horizons).
Zone of minor, iron-rich lenticular horizons.
<15mm
<120mm
INSECT LIMESTONE - very rare lenses. Typically thin with single 'round' example. Bedding noted.
16cm
23cm
Where lenses absent, bed traced by beige clay (~3cm).
Dark grey, finely laminated mud, conformable on undulose Insect Limestone.
INSECT LIMESTONE - discontinuous, lenticular bed.
34-54cm
5.5-6cm
Dark grey, finely laminated mud.
Iron-rich mud with discrete bivalve horizons (15mm; others one valve thick). Nestling of convex-up valves


BURNT WOOD (EAST)
cm
Lithology
Grain Size
clay
silt
fine sand
medium sand
coarse sand
Fossils
Description
140
135
130
120
115
110
105
100
95
90
85
80
75
70
65
60
55
50
45
40
5
Iron-rich, fossiliferous mud. Undulose. Fossils articulated, disarticulated (~15mm), and fragmentary bivalves. Rare intact gastropods (<20mm).
Finely laminated beige shale.
Irregularly disseminated bivalves (<12mm).
Blue-hearted, well indurated marl, weathering beige.
Laminated, beige mud.
Minor, iron-rich horizons (2-5mm).
Well indurated, beige marl. Lenticular.
Mud, blue-hearted fresh surface, weathering beige.
Minor iron horizons (~3mm) with secondary crystals.
INSECT LIMESTONE. Blue-hearted, weathering beige. Well indurated. Occasionally lenticular. Undulose lower contact. Concoidal fracture. Insect fossils rare; wings, body fragments.
Laminated, beige mud (3 to 6cm).
Iron-rich fossiliferous mud (5-9cm). Bivalves dominate (~2- 5cm); convex-up. Rare gastropod fragments (4-30mm). Rare oysters, at base, both intact (~25mm) and fragmentary. Erosive lower contact.


cm
Lithology
clay
Grain Size
silt
fine sand
medium sand
coarse sand
Fossils
GURNARD LEDGE
Description
124
120
115
110
105
100
95
90
80
75
70
65
60
55
50
45
40
35
15
10
5
Iron-rich, fossiliferous mud. Undulose. Fossils; articulated, disarticulated (~15mm), and fragmentary bivalves. Rare intact gastropods.
Massive Mudstone, weathering pale grey.
Discrete iron-rich lenticular horizons.
INSECT LIMESTONE Very rare lenses, only 2 noted at outcrop (GR462942). Where lenses absent, boundary between muds marked by iron-rich horizon ~1cm.
60 - 95cm
9 - 10cm
Finely laminated mud, weathering dark grey.
INSECT LIMESTONE Prominent, laterally continuous, blocky bed (40-75mm). Well indurated. Fresh surface blue, weathering beige. Concoidal fracture. Fossils rare; 2D insect fragments and small wings; 3D insects very rare; plant fragments common.
Dark grey mud, with thin (1-2mm), pale horizons . On exposed surfaces, single and aggregate crystals noted; opaque with brown tinge.
Iron-rich fossiliferous mud with grey irregularly rippled layers. Fossils; fragmentary bivalves (~25mm) gastropods (>2mm). Rare intact specimens (<40mm). Single layer of disarticulated bivalves (5-9mm).
Dark grey mud with discrete fossil pockets. Disarticulated (~7mm) and fragmentary bivalves. Intact gastropods (~5mm). Fish vertebrae.
Green-grey marl. Small intact gastropods common. Salt pseudomorphs on exposed surfaces.
BEMBRIDGE LIMESTONE Pale grey. Nodular appearance. Irregular upper contact. Rare intact gastropods.


Lithology
clay
Grain Size
silt
fine sand
medium sand
coarse sand
Fossils
NODE'S POINT
Description
125
120
115
90
85
80
75
70
65
60
55
50
45
40
35
30
25
20
15
10
5
Fe
&
S
Iron-rich, fossiliferous mud. Undulose. Fossils articulated, disarticulated (~15mm), and fragmentary bivalves. Rare intact gastropods.
Iron-rich lenses (~5 x ~2cm).
Dark grey dense shale, weathering light grey.
Iron horizon (1-4mm).
Dark brown mud. Salt pseudomorphs on exposed planes. Grades from indurate to soft from the Insect Limestone.
INSECT LIMESTONE Irregularly undulose (5.5 - 7cm). Heavily weathered to beige. Concoidal fracture.
Marl. Irregularly undulose bed, weathering beige.
Dark grey shale. Blocky
Extensive, iron and sulphur staining.
Fossiliferous horizon (intact bivalves and gastropod fragments).
Iron-rich fossiliferous mud (5 -8.5 cm).Fragmentary bivalves (<4cm) convex-up, dominate. Minor gastropod fragments.

APPENDIX 3

PALAEOGENE INSECT FAUNAS of NORTH AMERICA

Locality numbers refer to Figure 6.01.

taxon	1	2	3	4	5	6	7	8	9-11	12	13-15	16	17-21	22	23	24	25	27	28	29	30	31	32	33	35	36	37	38	39	40	41	43
Collembola	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**
Lepismatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Thysanura	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**
Poduridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ephemeroptera	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**0**
Ephemeridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Heptageniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Siphlonuridea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Baetidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Neoepheridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Odonata	**1**	**1**	**1**	**1**	**0**	**1**	**1**	**1**	**0**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**1**	**1**	**0**	**0**	**0**
Aeschnidae	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Agrionidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Anisoptera	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlorocyphidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlorolestidae	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corduliidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Calopterygidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epallagidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Gomphidae	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Libellulidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lestidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zacallitidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psocoptera	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**		**0**	**0**	**0**	**0**	**0**	**0**	**1**

Psocidae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epipsocidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Trichopsocidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Psyllipsocidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ectopsocidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Archipscoidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Myopsocidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Thysanoptera	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Aeolothripidae	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Embioptera	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**
Embiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Homoptera	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**1**
Achilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Adelgidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Aphididae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0
Cercopidae	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	1	1	0	0	0	0
Cicadellidae	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0
Cicadidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Cixiidae	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Coccidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Delphacidae	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fulgoridae	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	1
Pemphigidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psyllidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Ricaniidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tropiduchidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Heteroptera	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**1**	**1**	**1**	**0**	**0**	**1**	**0**	**1**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**1**
Acanthiidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphietomidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Belostomatidae	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Capsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Coreidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Corixidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Cydnidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Dipsocoridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Gelastocoridae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galgulidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gerridae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0
Hydrobatidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Lygaeidae	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Nepidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Notonectidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pentatomidae	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Reduviidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Saldidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Tingididae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Veliidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Neuroptera	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**
Chrysopidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Hemerobiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Inocellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Nemopteridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Osmylidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

Sialidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Rhaphidioptera	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**
Raphidiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Megaloptera	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**
Trichoptera	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**0**	**1**	**0**	**1**	**1**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**1**	**1**	**0**	**0**	**1**	**1**	**0**
Brachycentridae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydropsychidae	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hydroptilidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Leptoceridae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Limnephilidae	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0
Odontoceridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Phryganeidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0
Psychomyiidae	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sericostomatidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidoptera	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**1**	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**0**
Cossidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Elachistidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ethmiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Geometridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Nocturidae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Nymphalidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Papilionidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Phyllocnistidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pieridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Psychidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

Saturniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Thyrididae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tineidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Tortricidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Diptera	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**1**	**1**	**1**	**0**	**1**	**1**	**1**	**0**	**1**	**0**	**0**	**1**
Acroceridae	**0**	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agromyzidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Anisopodidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Anthomyiidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Asilidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Bibionidae	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	1	1	1	0	1	1	1	0	0	0	0	0
Blepharoceridae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bombyliidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Cecidomyiidae	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0
Cenopidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratopogonidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cestridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Chironomidae	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
Culicidae	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
Cyrtidae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cystidae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Dolichopodidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drosophilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Empididae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1
Eophlebomyiidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ephydridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Helomyzida	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0

Hiromoneuridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Lauxaniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Leptidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Milichiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Muscidae	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Mycetophilidae	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	0
Mydaidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Myopidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nemestrinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Oestridae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Otitidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Periscelidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Phoridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Piophilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pipunculidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Platypezidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Psychodidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ptychopteridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0
Rhagionidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Scatopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Sciaridae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0
Sciomyzidae	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Sepsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Simulidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Stratiomyiidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Syrphidae	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0
Tabanidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Tachinidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tephridae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Therevidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Tipulidae	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	1	1	0	0	0	1	0	1	1	1	0	0	0	0	0
Trichoceridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Trichoscelidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Trypetidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coleoptera	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**1**	**1**	**1**	**1**	**0**	**0**	**1**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**1**	**0**	**0**	**1**
Alleculidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	1
Anobiidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Anthicidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Anthribidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Bostrychidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Bruchidae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Buprestidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0
Byrrhidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Calandridae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Carabidae	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0
Cerambycidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Chrysomelidae	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1
Cicindelidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cistelidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cleridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Coccinellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Colydiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cryptophagidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cucujidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Curculionidae	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Dascyllidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Dermestidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1

Dytiscidae	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Elateridae	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1
Erotylidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Eucnemidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Histeridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	1	0	0	0	0	0	0
Hydrophilidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Lampyridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Lathridiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Lucanidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Lymexylidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Melandryidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Meloidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Melyridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Mordellidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Mycetophagidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Nitidulidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Nosodendridae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oedemeridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Otiorhynchidae	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parnidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Passalidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
Platypodidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Psephenidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Ptinidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Rhipiphoridae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Rhynchitidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rythidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Scarabaeidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0
Scotylidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0

Silphidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Staphylinidae	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1
Temnochilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Tenebrionidae	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0
Throscidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Mecoptera	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**
Bittacidae	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meropeidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Panorpidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hymenoptera	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**1**	**1**	**0**	**0**	**1**	**0**	**1**	**1**	**0**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**0**	**1**	**0**	**1**
Andrenidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Anthrophoridae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Apidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Aulacidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Belytidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Bethylidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Blasticotomidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Bombidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Braconidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	1	1	0	0	0	0	0
Cantharidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Cephidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ceropalidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Chalcididae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Chrysididae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cimbicidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cosilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cynipidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0

Diapriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Diprionidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Eurytomidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Eulophidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Evaniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Figitidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Formicidae	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	1	0	0	
Halicitidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Ichneumonidae	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	1	1	1	0	1	1	1	0	0	0	0	
Lydidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Megachilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
Melittidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Myrmicidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Oryssidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Pamphilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
Pergidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Pompilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Proctotrypidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Pteromalidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Scelionidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Scoliidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Siricidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Sphecidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	
Stephanidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Tenthredinidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	0	0	0	
Tiphiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	
Torymidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Vespidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	

Orthoptera	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**0**
Acrididae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0
Chorotypidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Gryllacrididae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Gryllidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Locustidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Locustopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Natidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Promastacidae	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prophalangopsina	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tettigonidae	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Blattodea	**1**	**1**	**1**	**1**	**1**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**0**
Blattellidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Blattidae	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0
Mantodea	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**0**
Mantidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Phasmatodea	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**0**
Phasmidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Phasmomimidae	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dermaptera	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**0**
Forficulidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Labiduridae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	1	0	0	0	0	0	0
Isoptera	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**		**1**	**0**	**0**	**0**	**1**	**0**	**0**	**1**		**1**	**0**	**0**	**0**	**0**	**1**
Hodotermitidae	**0**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0

| | | |

APPENDIX 4

SYSTEMATIC DESCRIPTION of the RIVERSLEIGH INSECTS

The morphological terminology and classification used here is that of 'The Insects of Australia' (C.S.I.R.O. 1992). The specimens have been described as far as possible. An open nomenclature is employed where further identification is problematic.

The abbreviation QM refers to the Queensland Museum, Brisbane.

Phylum ARTHROPODA
Superclass HEXAPODA Latreille, 1825
Class INSECTA Linné, 1758
Subclass PTERYGOTA Brauer, 1885
Division ENDOPTERYGOTA Sharp, 1899
Order COLEOPTERA Linné, 1758
Suborder POLYPHAGA Emery, 1886
Superfamily CURCULIONOIDEA Latreille, 1802
Family CURCULIONIDAE Latreille 1802?

Species A

Material. QM F16648, an incomplete adult with only head (partially encased in matrix) and prothorax present (Plate 7.7A). QM F34585 an incomplete adult with only damaged head and prothorax present.

Description.

Head. The head is large and produced forward into a broad, stout rostrum, about as long as the pronotum, although certainty is impossible since this feature is enshrouded in detritus. The compound eyes are large, bulging and situated dorsolaterally at the base of the rostrum.

Thorax. The prothorax is broad, half as long as wide, with gently convex lateral margins. The anterolateral corners of the pronotum project to form protective 'shoulders' about the head. The prosternum is bounded laterally by concave sternopleural sutures. The posterior margin of this plate curves round and between the fore coxae. The first pair of coxae are contiguous and meet along the midline. They are globular in shape and incorporate a lateral facing concavity to accommodate the femur.

Dimensions. Length of head and prothorax, 5mm.

Remarks. This species is refered to Curculionidae on the basis of its stout rostrum, large eyes towards the rostral base and contiguous, projecting, fore coxae. The incompleteness of the specimens prevents a more detailed interpretation.

Suborder POLYPHAGA Emery, 1886

Family indet.

Species B

Material. QM F34583, an incomplete adult, with only head and prothorax intact (Plate 7.7B). QM F34586, an incomplete adult, consisting only of the pronotum.

Description The body is highly convex in cross section.

Head - The head is hooded by the pronotum and is all but concealed from above. The anterior margin of the head is gently convex. The large, bulbous, compound eyes are ventrolateral in position, and approach the anterior margin (Plate 7.5K). The mouth is hypognathous.

Thorax - In plan view, the prothorax is a longitudinally elongate semicircle. The anterior margin is convex. On the ventral surface the sternopleural suture of the prosternum runs from the lateral margins of the head to the coxae of the first limbs. These sutures mark the lateral margins of the prosternum, which is bounded anteriorly by the head and posteriorly by the transverse suture of the mesosternal plate. The plate rises to an elevated process between the first pair of limbs. The sternopleural sutures of the mesothorax form a gently curved semicircular outline. The thorax slopes rapidly from the sternopleural sutures to the lateral margin of the prothorax.

Dimensions - Length of head and pronotum, 5mm.

Remarks. The specimens show a number of characters that support assignment to the Polyphaga: notopleural sutures are absent on the prothorax, the ventral portion of the notum (hypomeron) is joined directly to the sternum on each side along the notosternal suture, and the pleuron is reduced and concealed. Insufficient detail is preserved to allow a more detailed taxonomic assignment.

Suborder POLYPHAGA Emery, 1886

Superfamily HYDROPHYLOIDEA Latreille, 1802

Family HISTERIDAE Latreille, 1802

Species C

Material. QM F34582, an almost complete adult, with only mid and hind legs missing (Plate 7.7C).

Description. The outline of the body is a near perfect oval.

Head - The head is small (<one eighth body length) and subrectangular in outline, almost half as long as wide. The head is deeply sunk into the pronotum and is concealed

when viewed from above. The eyes are flattened and occupy the entire lateral margin of the head, approaching the anterior margin (Plate 7.5J). The mouth is hypognathous.

Thorax - A distinct pronotum, narrower than the meso- and metathorax, hoods the head. When viewed from above it appears rectangular in outline, and extends laterally beyond the head. The outline of the pronotum tapers gently from the posterior to the anterior margin. On the anterior margin of the prosternum is a raised median process which becomes a ridge running the length of the prosternum, decreasing in height as it does so. The first pair of limbs immediately flank this ridge. The pronotum and the mesonotum are united along a transverse suture. The mesosternum is bound laterally by the coxae of the second pair of limbs. Its anterior margin is marked by the boundary between the pronotum and the mesonotum, its posterior by the metasternal transverse anterior suture. The metasternal surface is divided along the midline by the longitudinal suture. Both the fore and hind coxae incorporate a concavity to accommodate the femur.

Abdomen - The abdomen tapers gently posteriorly, forming a rounded pygidium. The elytra are truncate leaving the propygidium and pygidium exposed. They do not meet, exposing a groove which runs the length of the meso- and metathorax to the propygidium of the abdomen. There are five sternites.

Dimensions - Length of beetle, 5mm.

Remarks. The ovoid body shape, truncate elytra exposing two complete tergites, and head all but concealed by the pronotum, are indicative of superfamilies Hydrophyloidea and Staphylinoidea. A median metasternal suture is unknown in the Staphylinoidea. The separation of the mid-coxae by more than the width of one coxa, and the wider separation of the hind coxae, indicate that the species belongs to the family Histeridae, and not Hydrophilidae.

Suborder ARCHOSTEMATA Kolbe, 1908

Superfamily CUPIDOIDEA Latreille, 1802

Family OMMATIDAE Newman, 1839

Species D

Material. QM F34595, an almost complete adult, missing head and prothorax, with the wings enshrouding much of the dorsal surface of the body (Plate 7.7D).

Thorax - The lateral margins of the mesothorax are parallel for much of their length, but begin to converge gently toward the anterior. The mesothoracic coxae are contiguous, globular in shape with a posterior-facing concavity. A median suture divides the metasternum. The primary wing attachments adjoin its anterior margin, the margin of the plate curving between and around them. The lateral metasternal sutures gently diverge

from the mesothoracic coxae, increasing the width of the plate posteriorly. The metathoracic coxae are larger than the mesothoracic but are not contiguous.

The dorsal surface is almost entirely shrouded by the exposed hind wings. They slope from the anterior 'shoulders' toward the midline. They do not meet but the gap separating them decreases in width posteriorly. The gap extends a quarter of the length of the thorax, at which point the wings meet. The cuticle within the gap displays a distinct terracing (Plate 7.4B). At the anterior margin is a small pinnacle posterior of which is a narrow ridge which runs the length of the gap.

The remains of the wings shrouding the dorsal surface show traces of venation (Plate 7.4A), but the detail is obscured by a coating of autolithified bacteria (Plate 7.6C).

Abdomen - The abdomen has a distinct blunt appearance, the lateral margins tapering gently to a rounded pygidium. The abdomen is covered by five tergites, the largest of which is the first. This tergite curves around and between the metathoracic coxae. The other four tergites are of relatively equal proportions.

Dimensions - Length of specimen, 7mm.

Remarks. This species is assigned to the suborder Archostemata on the basis of the metathoracic trochantins. The presence of five ventrites indicates that the species belongs to either Cupedidae or Ommatidae. The lack of grooves on the ventral surface to accommodate the legs precludes assignment to the Cupedidae, and indicates that the species belongs to the family Ommatidae.

Order TRICHOPTERA Kirkby, 1815

Family TASIMIIDAE?

Family indet.

Material. All the specimens represent incomplete larval stages (Plate 7.8; QM F34587, QM F34584 , QM F34588, QM F34589, QM F34590, QM F34591, QM F34592, QM F34593 and QM F34594).

Description. In cross section the dorsal surface is strongly curved, while the ventral surface is flattened.

Head - The head is globular in shape with a slightly flattened anterior margin, and is broader than long. The head is marked by two large ventrolateral antennal sockets, which protrude downwards. The scape of the antennae is large, and circular in cross section. The lateral epicranial sutures arise at the posterior margins of the head, pass around the sockets of the antennae on the lateral side and converge to form the median suture. The general outline of the suture is that of an inverted 'Y'. The epicranium is patterned by a random arrangement of setae emplacements. Five ocelli form a semicircle about a central ocellus toward the anterior margin of the head. The clypeal region, which is divided

transversely into two equal segments, is slightly produced and evenly convex over the entire margin. The sutura frontoclypealis is dorsally convex. The labrum is short and gently tapered. The mandibles are curved and opposable with a double saw-toothed edge. The ventral surface of the cranium is covered by a bilaterally symmetrical labium. Flanking this is a pair of gently convex maxilla (Plate 7.9B). Anterior to these, also flanking the labium, is a small, flattened eye of 'schizochroal-type' (Plate 7.5F, H).

Thorax - The thorax consists of three segments, the pronotum the largest of the three (Plate 7.8A). All are much wider than long, with the dorsal surface more heavily sclerotized than the ventral, and those of the abdomen. There is a distinct ridge around the periphery of the pronotum. There are three distinct zones to each tergite which are recognizable. The anterior prescutum (Plate 7.3A) is relatively narrow but increases in thickness dorsally, forming a 'saddle-like' feature and patterned by a irregular arrangement of holes (Plate 7.3B). The scutum, the largest of the three units, is patterned by a random arrangement of raised setae emplacements. The posterior scutellum is wider than the prescutum although similarly patterned (Plate 7.3C). The scutellum of one segment overlies the prescutum of that behind. The individual tergites are separated by intersegmental membranes. A large spiracle is present on the lateral surface of the pronotum. There is a slight bulging of each segment laterally, just above the first pair of limbs. The limbs themselves are robust and decrease in size posteriorly. The base of each limb is protected by a coxal collar (Plate 7.3D). The adjacent arthrodial membrane is distinctly patterened (Plate 7.3 E, F)

Abdomen - The abdomen bears at least nine tergites, although no complete specimen exists. There is a slight swelling of the abdomen about the fifth tergite and it tapers gently posterior to this. The scutellum of each tergite overlaps the prescutum of the following one, as with the thorax. The last few tergites have a distinctive appearance, the penultimate segment bearing by two posteriorly projecting conical 'horns' on the dorsal surface (Plate 7.9 C, D). The final tergite terminates in a hemispherical 'bulb' (although this may be an evacuation of internal tissue, since this 'bulb' is absent from a second specimen. A tube-like spiracle projects posteriorly from the ventral surface of each abdominal somite. The cuticle of the abdomen, including that of the tergite with the 'horns', is ornamented in a similar fashion to the thorax. The only difference is the presence of small 'fang-like' posteriorly projecting barbs on the prozonite. These barbs decrease in size towards the ventral surface, where they are absent. On the ventral surface are small, longitudinally aligned setae.

Dimensions - Almost complete specimens suggest an overall length of 50 to 70 mm.

Remarks. The orders Trichoptera and Lepidoptera are united in the informal rank Amphiesmenoptera. Accordingly the larvae possess many similarities. However, the presence of a pair of projecting conical 'horns', or terminal abdominal prolegs, allows the Riversleigh species to be assigned to the order Trichoptera with some certainty. More

detailed taxonomic assignment would require information on the position of setae or spicules on the abdomen.

Class MYRIAPODA Latreille, 1796

Order JULIDA Brandt, 1833

Family indet.

Material. QMF34596 x2, mid sections of the trunk composed of four and five segments respectively.

Description.

Trunk - The trunk consists of a number of leg-bearing rings. The sclerites of each ring are fused together and to the pleurotergal arch to form a completely cylindrical sclerite (Monozonian condition). The prozonite of one ring is overlapped by the metazonite of that preceding it. The two zonites are separated by a distinct suture. Each ring carries two pairs of limbs and constitutes a diplosegment. The coxal openings are small and project laterally. The limbs are slender.

Dimensions - Length of single ring 3mm, diameter 4mm.

Remarks. The presence of only disarticulated segments precludes assignment beyond the level of suborder.

APPENDIX 5

SAMPLE EXPERIMENTAL CHECKING SHEET

SPECIES
SPECIES NO.
RUN TYPE

TEMPERATURE

WATER

SEDIMENT

RUN
STARTED
SAMPLED
CONCLUDED

pH
INITIAL
FINAL

WEIGHT
INITIAL
FINAL(DRY)

•CONDITION OF WATER

•GENERAL MORPHOLOGY OF SPECIMEN

HEAD •GENERAL

•COMPOUND EYE
•ANTENNAE
•MOUTH ORGANS

THORAX •GENERAL

•TRUNK

•LEGS

•WINGS ELYTRA
HIND

•MUSCULATURE

ABDOMEN•GENERAL

•TERGITES
•CERCUS/(OVIPOSTER)
•INTERNAL ORGANS GENERAL

HEART
CROP
GANGLION

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